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VARIATION IN STEM DIAMETER INCREMENT AND ITS EFFECT ON TAPER IN CONIFERS

BY

MERLISE A. CLYDE

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

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EDMONTON, ALBERTA

FALL 1986

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Merlise A. Clyde

Merlise A. Clyde

1705 N. Madison

El Dorado, Arkansas 71730 USA

Date: May 27, 1986

THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled VARIATION IN STEM DIAMETER INCREMENT AND ITS EFFECT ON TAPER IN CONIFERS submitted by Merlise A. Clyde in partial fulfilment of the requirements for the degree of Master of Science.

S. J. Titus
Supervisor

Victor Jeffers

Robert T. Hanlon

Date: May 20, 1986

ABSTRACT

Variation in annual diameter increment is compared for lodgepole pine, white spruce, and black spruce in Alberta using three-dimensional graphs of diameter increment at various ages and heights along the stem. Differences in the form of the diameter increment surface may be explained by crown class and shade tolerance of the different species within a single stand. An individual-tree mathematical model based on the Chapman-Richards growth curve is developed to predict diameter increment as a function of age and height along the stem. Diameter increment from sections at various heights along the stem is modelled as a function of age using the increment form of the Chapman-Richards growth curve. Parameters for each of the sections were re-expressed as functions of height to obtain a continuous model over height and age. This growth model is used to derive estimates of stem taper and volume over time. Diameter increment models were also derived as the first derivative of four existing taper equations. The predictions of diameter increment from these models are reasonable but not always consistent with observed growth data, particularly near the base and tip of trees.

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GENERAL INTRODUCTION

Background

Taper equations have been developed to describe diameter or stem cross-sectional area as a function of height along the stem, using diameter at breast height (DBH) and total tree height as independent variables (Kozak et al. 1969). These equations can be integrated to provide estimates of stem volume for any portion of the tree. Most individual-tree growth and yield models incorporate equations for predicting future values of DBH and total height. These predicted values are often used in conjunction with a taper model to obtain estimates of future volume (Arney 1985).

When a taper model is used as a component of a growth and yield model to obtain the stem profile and volume of a tree in the future, an implicit relationship is defined for diameter increment along the stem. In practice, it is usually assumed that knowledge of the change in DBH and height will adequately describe the change in upper stem diameters. However, the change in diameter at one position (i.e. DBH) usually is not representative of diameter increment elsewhere along the stem (Kramer and Kozlowski 1979). Loetsch et al. (1973) compared upper stem diameter increment to the increment at breast height after a heavy thinning. Using only the DBH and height increment resulted in overestimating volume increment by about 10 percent. There have been, however, few quantitative studies examining

diameter growth rates at various heights along the stem throughout a tree's life, and how this relates to stem taper (Arney 1972, 1974; Mitchell 1975). Improvements in modelling the stem profile and volume can be made by taking into consideration the variation in diameter increment along the stem. Since the accumulation of diameter increment results in diameter, this is the logical starting point for modelling diameter, taper, and volume development over time.

Several descriptive studies have examined radial and longitudinal variation in diameter increment in conifers (reviewed by Larson [1963]). Duff and Nolan (1953, 1957) classified the longitudinal variation in annual diameter increment as a Type 1 sequence. Starting from the tip of the tree, diameter increment increases to a maximum near the crown base or the area of maximum branch development (Farrar 1961). Below this point diameter increment remains constant or decreases in the area of the clear bole, and then increases toward the base of the tree. Duff and Nolan (1953, 1957) described the radial pattern in diameter increment at one height as a Type 2 sequence. Starting from the center of the tree, this sequence increases towards a maximum and then declines with increasing age. Because diameter increment depends on the location along the stem and age (or number of rings from the center), a better understanding of change in diameter increment can be obtained by considering spatial and temporal patterns of variation simultaneously. Fayle (1973) constructed surfaces to represent diameter increment at various heights and ages, and

graphed the data as in a topographic map, using contour lines to connect equal diameter increments. In a logical extension of this method, Thomson and Van Sickle (1980) and Julin (1984) used computer graphics to construct three-dimensional surfaces of diameter increment and area increment. Although Julin (1984) claims area increment represents growth more closely than diameter increment, only diameter increment was examined here because area increment depends on the present diameter increment and the previous year's diameter (Assmann 1970). Because the previous diameter is the sum of past diameter increments, area increment combines the effects of present and past disturbances and reflects cumulative size over time. This results in autocorrelation of area increment in successive time periods, a problem when regression methods are used for modelling.

Study Objectives

To date, little effort has been made to model diameter increment along the stem over time. From the literature, there is evidence that there should be a fairly well defined pattern for diameter increment within an individual tree. However, there is a large amount of tree to tree variation when diameter increment from several trees is examined. Because there is a clear relationship for growth within a single tree, this study will examine the following questions from an individual-tree perspective.

1) Are there qualitative differences in the diameter increment surface for trees of different species and crown classes within a single stand?

2) Can a mathematical model of the diameter increment surface be developed based on the Duff and Nolan (1953, 1957) Type 1 and 2 sequences?

3) What increment model is implied by existing taper models and do they make reasonable predictions?

Diameter increment data for lodgepole pine (Pinus contorta var. latifolia Engelm.), white spruce (Picea glauca [Moench] Voss), and black spruce (Picea mariana [Mill.] B.S.P.) trees from the foothills of Alberta were used to examine these questions. Once there is a better understanding of changes in diameter increment within an individual tree, then reasons for differences among trees can be examined. The general approach to addressing these questions is given in the next section.

General Approach

The growth and development of different species can be compared by examining diameter increment surfaces for individual trees. The three-dimensional representation of diameter increment, height, and age can illustrate how Type 1 sequences change in form as the tree ages, and how Type 2 sequences vary

in a progression up the stem. A better understanding of this process can aid studies examining the effects of silvicultural treatments on the distribution of diameter increment along the bole, and can assist those developing mathematical models of the process for growth and yield models. The first chapter of this thesis examines differences in growth and development among three coniferous tree species, and among crown classes within species.

In the second chapter of this thesis, a mathematical model is developed to predict diameter increment as a function of stem height and age. Taper equations are often based on empirical models with little biological basis. When used in growth projection, it would be ideal if taper models predicted diameter increment along the stem consistent with observed patterns of diameter increment. This is important especially where the effects of thinning and fertilization or other treatments may be different at DBH than at other positions along the stem (Arney 1972, 1974; Loetsch et al. 1973). Arney (1972) developed a model for diameter increment along the bole, however his model is based on measurement of upper stem diameters at various ages for several different trees, not on a true time series of diameter increment. His model does not account for the increase in diameter increment near the base of the tree nor the butt swell. Mitchell (1975) determined bole increment as a proportion of foliage volume, and used this to determine area increment along the stem according to Pressler's Growth Law (Larson 1963). Within the crown, area increment increases

linearly from the tip of the tree to the crown base, and remains constant from the crown base to the base of the tree. This model does not account for the increase in area or diameter increment near the base of the tree. It is not known whether Arney's (1972) or Mitchell's (1975) models predict diameter increment over time that is consistent with the observed patterns of radial variation in diameter increment.

A model to predict stem diameter increment based on the Duff and Nolan (1953, 1957) Type 2 sequences at various heights should give biologically consistent estimates of taper and volume over several ages. Each Type 2 sequence can be represented as the increment form of a sigmoid growth curve. By expressing the parameters of the growth curve obtained at each height as a function of height along the stem, a continuous model for diameter increment at any height and age can be obtained. Derivation of this model and its ability to predict changes in stem profile and volume over time are presented.

An alternative approach to develop a stem diameter increment function is presented in the third chapter. Basic calculus shows that the derivative of a function may be integrated to obtain the function. If there is some function that is a continuous function of time that represents cumulative size or yield, then the derivative of that function represents growth. This is the approach first applied to forestry by Clutter (1963). The same approach is used here to derive and study the diameter increment functions implied by several published taper models. When a taper model is used as a component of a growth

and yield model, it implicitly defines an equation for diameter increment along the stem. If both DBH and total height are functions of time, then a model for diameter increment as a function of time and height along the stem can be derived from a standard taper model by taking the first derivative of the taper equation with respect to time. Four standard taper models are used to derive diameter increment functions. Predictions from these models are examined to determine the accuracy of existing taper models for predicting diameter increment along the stem.

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VARIATION IN STEM DIAMETER INCREMENT OF CONIFERS: SPECIES AND CROWN CLASS DIFFERENCES

INTRODUCTION

Several descriptive studies have examined the distribution of annual ring or area increment along the stem in conifers (Duff and Nolan 1953, 1957; Farrar 1961; Larson 1963; Fayle 1985). Duff and Nolan (1953) classified the longitudinal pattern of diameter increment as a Type 1 sequence. For a single year's growth, the ring widths gradually increase from the top of the tree to the most productive part of the crown or area of maximum branch development (Farrar 1961; Wilson 1970). From this point the ring widths slowly decline to a minimum or may remain constant. Toward the base of the tree, the ring widths increase again, reaching a second maximum. The Duff and Nolan (1953) Type 2 sequence describes the series of ring widths at one height, beginning with the year the tree reached that height through to the most recent annual ring produced. This series quickly increases to a maximum and then declines exponentially. These two sequences describe temporal and positional changes in diameter.

Three-dimensional graphics have been used to describe how diameter and area increment vary with age and height along the stem (Fayle 1973; Thomson and Van Sickle 1980; Julin 1984). The three-dimensional representation is an improvement over the methods of Duff and Nolan (1953, 1957), as it integrates

temporal and positional growth patterns in an informative graphic format, so both the Type 1 and Type 2 sequences can be viewed simultaneously. In this chapter, three-dimensional graphics of diameter increment, height, and age are used to compare growth and development of trees of different species and crown classes in mixed species stands of lodgepole pine (Pinus contorta var. latifolia Engelm.), white spruce (Picea glauca [Moench] Voss), and black spruce (Picea mariana [Mill.] B.S.P.) in Alberta. The graphical information was also used to examine differences in stem form, since stem form is the result of annual accumulation of Type 1 sequences.

DATA COLLECTION

Stem analysis disks were obtained from the Alberta Forest Service for 36 lodgepole pine (11 dominants, 22 codominants, 3 intermediates), 12 white spruce (6 dominants, 3 codominants, 3 intermediates), and 27 black spruce (4 dominants, 14 codominants, 7 intermediates, 2 suppressed) trees located in three stands east of Grande Cache and eight stands south of Grande Prairie, Alberta. All plots were in mixed-wood stands consisting of lodgepole pine, white and black spruce, and balsam fir (Abies balsamea [L.] Mill.) with a minor component (less than 20 percent of stand volume) of aspen (Populus tremuloides Michx.). Site conditions ranged from fair to good, with seven of the eleven sampled plots classified as medium site (Alberta Energy and Natural Resources 1985).

Sections were removed at the stump (0.3 m), breast height (1.3 m), and at 2.5 m intervals above the stump section. Ages at the stump ranged from 79 to 147 with a mean of 115. Sections were brought back from the field for detailed measurements of diameter increment. The number of annual rings was determined for each section and annual radial increments were measured to the nearest 0.01 mm along the longest and shortest axes using a computerized tree ring measuring device (Appendix A). Annual diameter increment was calculated as twice the arithmetic mean of the four radial increments. During data collection, visual data editing was possible by plotting Type 1 and 2 sequences, height-age curves, and three-dimensional graphs of diameter increment, height, and age for each tree using Plot88 software (Plotworks Inc., La Jolla, California). Relative comparisons among trees were made by scaling the three axes of the three-dimensional graphs to the same length for each tree.

RESULTS AND DISCUSSION

General Form of Diameter Increment Surface

The three-dimensional surface of diameter increment, height, and age (Fig. 1.1) offers insights into the growth and development of a tree that are not readily apparent from just the Type 1 and 2 sequences. By taking a vertical "slice" from the surface parallel to the height axis (at one age), a Type 1 sequence is obtained. By vertically slicing the surface

parallel to the age axis, a Type 2 sequence is obtained. It is evident that during certain years, conditions were not as favorable for diameter growth, causing "troughs" or "valleys" running parallel to the height axis. Likewise, one can also see "ridges" which formed when conditions were better. Valleys and ridges may be caused by disturbances such as fire, defoliation, climatic variation, and release from nearby trees (Thomson and Van Sickle 1980). A disturbance at one position may affect growth for several years, as well as influence growth all along the stem.

Another aspect shown in the diameter increment surface is that the maximum diameter increment at each height increases with height to a maximum and then declines exponentially toward the tree tip. The number of years from the center to when the maximum diameter at each height occurs decreases exponentially up the stem, so eventually the first ring formed has the maximum diameter increment, with following increments decreasing with time. This is illustrated better in the individual Type 2 sequences (Fig 1.2) or by changing the viewing angle of the three-dimensional surface. The form of the Type 2 sequence at different positions along the stem changes in a fairly regular manner with increasing height, with most of the growth occurring lower on the stem. In older trees the Type 2 sequences near the top of the tree tend to flatten out (Fig 1.1). Another trend is that the Type 1 sequences tend to become flatter as the tree ages, indicating that diameter increment becomes more evenly distributed along the stem (Fig 1.1). At earlier ages most of

the diameter increment from the longitudinal series is distributed along the upper part of the stem. In all of the trees examined the diameter increment continued to increase toward the tip of the tree, never decreasing after reaching a maximum as reported by others (Duff and Nolan 1953, 1957; Farrar 1961; Fayle 1985). This may be related to the measurement interval, length of live crown, and/or site quality. It is possible that the maximum value occurred within the interval between sampling points along the stem. Trees with small crowns on poor sites tend to have most of the annual increment distributed towards the top of the tree (Larson 1963). Although crown characteristics cannot be reconstructed from stem analysis data, the pattern of increasing diameter increment with increasing height was observed on both good and poor sites.

Species Comparisons

The same general form was evident in the diameter increment surface for the three species examined, but the distribution of diameter increment differed (Fig. 1.3). Lodgepole pine reaches the maximum diameter increment at a given height fairly rapidly and then quickly decreases. In contrast, with white spruce and black spruce, diameter increment does not decline as rapidly after reaching the maximum. Relative to the maximum diameter increment produced, the spruces are able to maintain higher and more constant levels of diameter increment over time. This is probably due to the shade tolerance of the different species.

Lodgepole pine is a shade intolerant species, which suggests that it must put on most of its growth at an early age to successfully colonize and dominate the site (Fowells 1965; Spurr and Barnes 1980; Heinselman 1981), and the growth rate sharply declines as it faces increased competition and is eventually replaced by spruce. This was evident in all of the lodgepole pine trees examined, regardless of crown class.

The spruces are more tolerant of shade, permitting them to maintain greater relative diameter increments in the presence of competition. Because the lower branches on tolerant trees retain foliage longer (Larson 1963), relative diameter increment is greater over the length of the stem and is maintained at a higher level for a longer period of time than in lodgepole pine. The mixed-species stands sampled are single-storied, so that the decline in growth at a given height may be due to increasing crown competition at that height. More tolerant species are able to withstand more competition, so their decline in growth occurs later. Assmann (1970) reported that maximum height growth occurs earlier in light-demanding species than shade tolerant species, similar to results obtained here for diameter growth.

Crown Class Comparisons

Within species, differences were observed in the diameter increment surface among trees in different crown classes (Fig. 1.4). In general, dominant trees of all species were able to

maintain growth near the level of the maximum diameter increment at a given height for a longer period of time than codominants, intermediates, or suppressed individuals. Dominants are classified as trees with crowns extending above the general level of the canopy and receiving full light from above and partly from the sides (Spurr and Barnes 1980). Because their crowns receive more light from the sides and less competition from other crowns, dominants should maintain the maximum diameter increment at a given height for a longer time. Diameter increment at a given height declines over time as in other crown classes as crowns receive more competition from the sides. The crowns of codominants form the general level of the canopy and growth rates drop off at a more rapid rate than in dominants, as they are getting direct light only from above. Because the crowns of intermediate trees are within the canopy and receive even less light, diameter increment drops off rapidly after reaching a peak at each height.

Differences among crown classes in the form of the surface were greater in the spruces than in lodgepole pine. Although the reasons are not clear, this may be due to differences in rates of height growth and shade tolerance. On the lower part of the stem, the maximum diameter increments at each height do not occur initially, but occur when that particular height will be shaded from above and from the sides. In general, height growth rates for spruce are less than the rates for lodgepole pine during the period of time when these maximum diameter increments occur. If the decrease in diameter increment at a

particular height is due to the effects of crown shading at that height, a particular point along the stem will become self-shaded earlier in pine than in spruce because height growth in pine is greater. Assuming equal amounts of shading from neighbors, diameter increment will drop off more rapidly in pine than in spruce, because of higher levels of self-shading and the shade-intolerance of foliage. Because pines are shade-intolerant, this decrease should occur fairly soon after the maximum is reached at a given height, so one would expect few differences among crown classes in pine, as was observed. Because their height growth is slower, spruces will be self-shaded later, but would likely receive more shading from the sides because of the slight lag in height growth with the pines. However, shade-tolerant foliage would allow growth to continue nearer the maximum for a longer period of time. Crowns of codominants, intermediates, and suppressed individuals receive less light from above depending on the crown class. Growth drops off much earlier in suppressed trees because of exponential light decay through the canopy. The form of the surface for pine is similar to the intermediate crown class in spruce.

Development of Taper

Because the taper of a tree is the result of annual accumulations of the Type 1 series, some insight into the development of stem taper can be gained by examining the

diameter increment surface. Butt swell will occur when diameter increment near the base of the tree is greater than diameter increment above it over a period of time. Lodgepole pine develops less butt swell and takes longer to develop it than the spruces. Generally, the more shade tolerant, longer crowned species, such as the spruces, will have a more pronounced butt swell and more taper (Larson 1963).

In younger trees, the greater height growth and the steeper slope of the Type 1 sequence in the upper part of the stem result in a slightly conic form or more taper. As height growth declines, a more constant amount of diameter increment is added over most of the stem with increasing age (i.e. the Type 1 sequence flattens) except at the base and the tip, so that as the tree gets older the main bole does not change as much, becoming more cylindrical. However, because there is still an increase in diameter increment near the base of the Type 1 sequence, even in the older trees, the butt swell becomes more pronounced. In lodgepole pine the Type 1 sequence becomes more constant over most of the stem earlier than in the spruces, so that the main stem becomes less tapered in pines.

Conclusions

Three-dimensional representation of the diameter increment surface allows one to veiw changes in diameter increment over time and at various positions along the stem. In addition, qualitative comparisons can be made among species and within

species among different crown classes. Differences among species in the form of the diameter increment surface can be explained by shade tolerance. Differences among crown classes are also related to shading effects. Knowledge of how diameter increment changes with time and position along the stem can be used to examine changes in stem form with age. A better understanding of this process will aid study of the effects of silvicultural treatments, such as thinning, fertilization, or disturbances on changes in stem form. In addition, the well defined pattern in the Type 1 and 2 sequences can be used as a basis for deriving a system of diameter increment, taper, and volume equations, based on the basic growth process of diameter increment.

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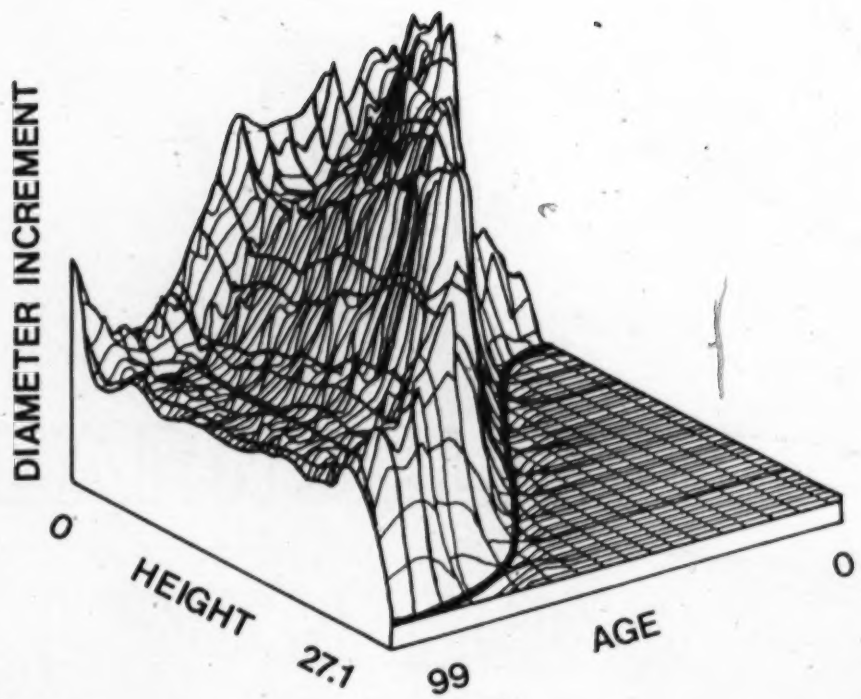

Figure 1.1. Three-dimensional graph of diameter increment, height, and age for a dominant white spruce. Bold line in the height-age plane is the height-age curve.

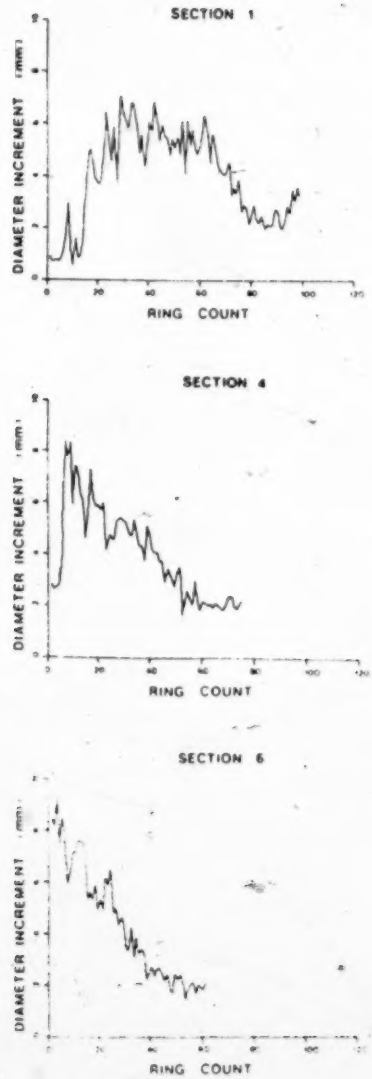

Figure 1.2. Type 2 sequences at various heights along the stem for the dominant white spruce illustrated in Fig. 1.1.

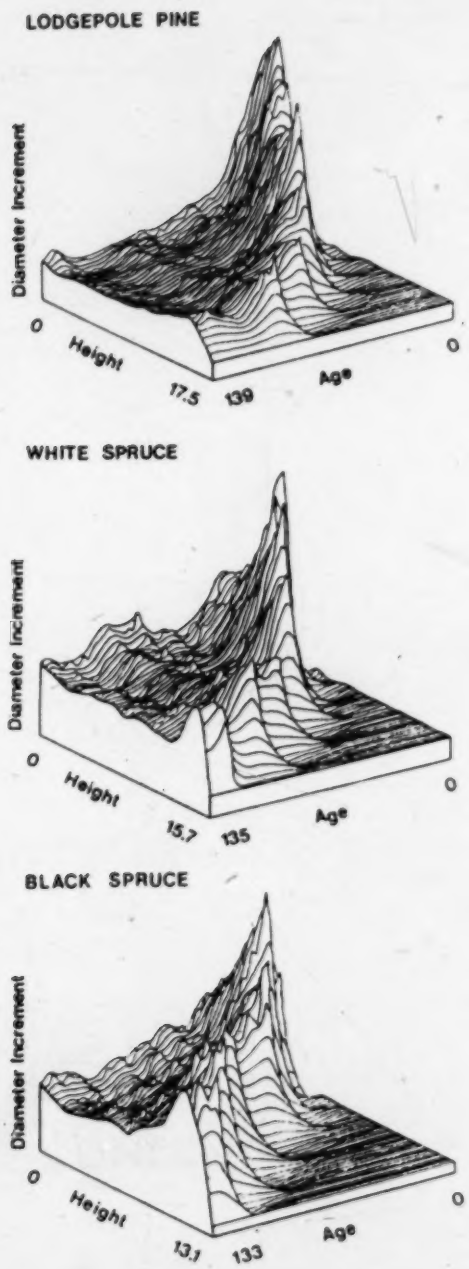

Figure 1.3. Three-dimensional graphs of diameter increment, height, and age for codominant lodgepole pine, white spruce, and black spruce trees on the same site.

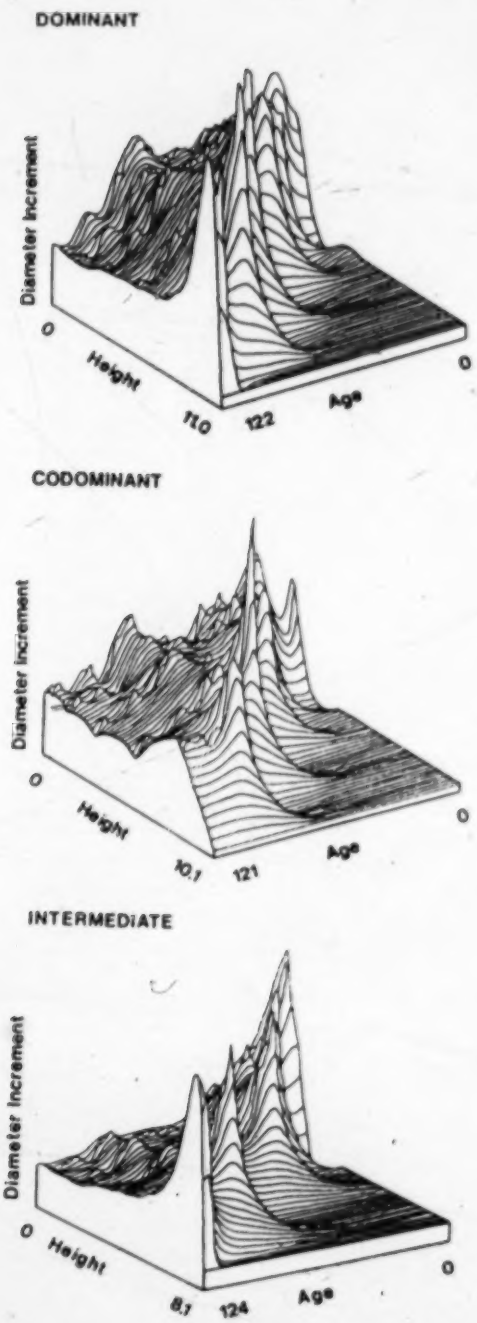

Figure 1.4. Three-dimensional graphs of diameter increment, height, and age for dominant, codominant, and intermediate black spruce trees on the same site.

A STEM DIAMETER GROWTH MODEL FOR CONIFERS

INTRODUCTION

Forest growth and yield studies have concentrated on modelling diameter at breast height (DBH) and height growth over time to determine future stem taper and volume using taper equations. It is assumed that the taper models do not change over time, so that predictions of future stem diameters depend only on knowledge of the future DBH and total height. Unfortunately, diameter measurements made at a single height do not accurately measure growth along the entire stem (Kramer and Kozlowski 1979). Little attention has been devoted to modelling diameter or area growth along the entire tree profile (Arney 1972, 1974; Mitchell 1975; Thomson and Van Sickle 1980).

Arney (1972, 1974) and Mitchell (1975) examined diameter or area increment along the stem as a component in individual-tree distance-dependent growth models. Arney (1972) modelled outside-bark stem diameters (DOB) as a linear function to determine the maximum future diameter at a given height,

$$DOB = b_0 + b_1(AGE_D) + b_2(L),$$

where AGE_D is stem age at the DOB measurement point and L is the length from the tip of the tree to the DOB measurement point. The maximum annual diameter increment (ΔDOB) was determined by taking the first difference of the above equation,

$$\Delta DOB = b_1 + b_2(\Delta L),$$

where ΔL is the current annual increment in stem length. This

maximum diameter increment was then multiplied by a crown competition quotient for each whorl to determine the stem diameter increment at each whorl. Below the live crown base the model assumed the stem area increment remained constant, so that diameter increment decreased toward the base. In Mitchell's (1975) model, stem area increment is assumed to increase linearly from the tip of the tree to near the crown base, and from there is a constant value based on Pressler's "law of stem formation" (Larson 1963). However, area increment in the clear bole remains constant only in a few cases and for limited distances along the stem (Larson 1963; Assmann 1970). Neither model accounts for the increase in diameter or area increment at the base of the tree and the resulting butt swell.

Duff and Nolan (1953, 1957) classified the pattern of variation in diameter increment along the stem as a Type 1 sequence. For a single year, this sequence is represented by a pattern of ring widths that gradually increases from the tip of the tree to a maximum near the point of maximum branch development (Farrar 1961; Wilson 1970), slowly declines or remains constant along the clear bole, and then increases toward the base of the tree. The Duff and Nolan (1953) Type 2 sequence describes the series of ring widths at one height, beginning with the year of formation through to the last annual ring the tree produced. This sequence reaches a maximum fairly quickly and then gradually decreases with increasing age.

Although the Type 2 sequences vary considerably at different heights along the stem, as discussed in Chapter 1, there is a

fairly regular trend in the change of the form of the Type 2 series with increasing height. Generally, in a progression up the stem, the maximum diameter increment at each height occurs at an earlier ring count, where ring count is the number of years from the center of the section. Eventually, near the top of older trees, the maximum diameter increment is formed first. The maximum diameter increment at each section increases with height to a maximum and then declines exponentially toward the tip of the tree. The largest growth rates occur lower on the stem at an early age, while the Type 2 sequences toward the tip of older trees are fairly flat. At later ages, the Type 1 sequences tend to flatten out so that a more constant increment is added along the stem. Based on the observed processes for Type 1 and 2 sequences, and how they vary with height and age, a model is developed to accurately predict stem diameter increment at any height and age. With this model, changes in taper and volume over time that are consistent with the underlying growth processes for diameter and height can be predicted.

DATA COLLECTION

The study area was located approximately 40 km east of Grande Cache, Alberta (53°49' N, 118°30' W) on a well-drained site. Conifers made up 59 percent of the total vegetative coverage, with an overstory consisting of white spruce (Picea glauca [Moench] Voss), lodgepole pine (Pinus contorta var. latifolia Engelm.), black spruce (Picea mariana [Mill.] B.S.P.),

and balsam fir (Abies balsamea [L.] Mill.). Mean diameter for all species was 20.95 cm (range 9.4 to 28.4 cm) and the average height of dominants and codominants was 16.8 m (range 6.0 to 19.8 m).

Stem analysis disks were obtained from the Alberta Forest Service for one dominant and four codominant lodgepole pine trees from the stand. Ages ranged from 139 to 147 years (mean = 141) at the stump, with total heights of 13.7 to 18.9 m (mean = 16.3). Average DBH for sectioned trees was 23.6 cm (range 19.0 to 32.0 cm).

Sections were removed at the stump (0.3 m), breast height (1.3 m) and at 2.5 m intervals above the stump section and brought back from the field for detailed measurement of diameter increment. The number of annual rings was determined for each section, and annual radial increments were measured to the nearest 0.01 mm along the longest and shortest axes using a computerized tree ring measuring device (Appendix A). Annual diameter increment was calculated as twice the arithmetic mean of the four radial increments. Type 1 and 2 sequences, taper profiles at various ages, a height-age curve, and a three-dimensional graph of diameter increment, height, and age were plotted for each tree to visually check for measurement errors.

MODEL DEVELOPMENT

In general, cumulative diameters (D) over time (t) at various heights along the stem can be modelled using a sigmoid

growth curve,

[1] $D = F(\underline{\theta},t)$,

where $\underline{\theta}$ represents four parameters ($\underline{\theta}_1$, $\underline{\theta}_2$, $\underline{\theta}_3$, $\underline{\theta}_4$) (the underline is used to represent a vector). The number of rows in $\underline{\theta}$ equals the number of sections taken for each tree. The diameter increment time series (D_{inc}) for all sections, the Duff and Nolan (1953) Type 2 sequence, can be modelled as the increment or rate form of [1],

[2] $D_{inc} = F'(\underline{\theta},t)$.

Equation [2] can be used to describe how diameter increment changes over time at discrete heights along the stem. However, a continuous model for diameter increment for any time and height along the stem can be obtained by re-expressing the matrix of parameters $\underline{\theta}$ as functions of height along the stem.

Many sigmoid growth curves have a parameter which is the asymptotic size the individual will eventually approach as time increases. In the case of the Type 2 sequences, this parameter would be the diameter that the tree would eventually approach at that height. By considering each height along the stem, the asymptotic size parameters ($\underline{\theta}_1$) would represent the diameters (D_∞) at various heights the tree would eventually approach and can be re-expressed as a function of height, as an asymptotic taper model.

Another parameter ($\underline{\theta}_2$) used in [2] would be the initial age (t_0) at which increment begins at each height. Diameter increment would begin once the tree reaches that height. Thus, t_0 would be the age the tree reaches the total height (H). If

the height-age curve is,

[3] $H = G(\underline{\chi}, t_0)$,

then t_0 is obtained as the inverse of the height-age curve,

[4] $t_0 = G^{-1}(\underline{\chi}, t_0)$,

with parameters $\underline{\chi}$. So the vector $\underline{\theta}_2$ can be replaced by [4].

The maximum diameter increment ($D_{inc\ max}$) at each height and the time at which it occurs (t_{max}) change in a regular manner with increasing height along the stem, as discussed in Chapter 1, and can be expressed in general terms as functions of height along the stem (h),

[5] $D_{inc\ max} = g(\underline{\alpha}, h)$

[6] $t_{max} = f(\underline{\chi}, h)$,

where $\underline{\alpha}$ and $\underline{\chi}$ are two vectors of parameters to be estimated. Both $D_{inc\ max}$ and t_{max} can be determined mathematically for each section from [2],

[7] $t_{max} = t \mid F''(\underline{\theta}, t) = 0$

[8] $D_{inc\ max} = F'(\underline{\theta}, t_{max})$.

Since both $\underline{\theta}_1$ and $\underline{\theta}_2$ can be expressed as two functions of height as discussed above, they can be eliminated from [7] and [8]. Thus, [7] and [8] depend only on values of parameters $\underline{\theta}_3$ and $\underline{\theta}_4$. These two parameters of the growth curve can be re-expressed as functions of height by setting [5] equal to [8] and [6] equal to [7] and simultaneously solving for these two parameters as functions of height.

A continuous model for diameter increment can be developed from the individual Type 2 sequences, using $D_{inc\ max}$, t_{max}, t_0, and the asymptotic taper to obtain the four parameters ($\underline{\theta}$) as

functions of height. Cumulative diameters or the stem taper at various ages can also be obtained by substituting the functions for $\underline{\theta}$ into [1]. Stem volume for a given age is obtained by integration of stem cross-sectional areas over height and can be obtained from [1].

For estimating parameters, the increment form of a growth curve is more appropriate than the cumulative form because of autocorrelation among successive sizes when measurements are made over time on the same individual (Moser 1967; Gertner 1981). In ordinary least squares regression, parameter estimates are unbiased, but inefficient if autocorrelation is present. However, when nonlinear regression is used it is not clear if this property holds if there is autocorrelation in the dependent variable or errors (Gertner 1981). Because there are more differences in the increment forms of the growth curves than in the cumulative versions, the use of the increment curves may be more selective in determining the appropriate model. Although Julin (1984) claims area increment may represent growth more closely than diameter increment, autocorrelation is a problem when modelling area increment because area increment depends on the present diameter increment and the diameter of the previous time period (Assmann 1970). For this reason, only diameter increment was considered in development of this model. Cumulative diameters and areas are functions of diameter increment and can be determined later.

Since an objective of this study was estimation of diameter and volume, it was desirable that the diameter increment model

could be integrated. Because the location or ring count at which the maximum diameter increment occurred (inflection point of the cumulative diameter curve) varied with position along the stem, as shown in Chapter 1, it was necessary to use a fairly flexible function. A growth curve generally requires four parameters for the inflection point of the curve to vary (Hunt 1982). Preliminary analysis indicated that the increment form of the Chapman-Richards generalization of the von Bertalanffy growth curve (Richards 1959; Pienaar and Turnbull 1973) was appropriate for modelling diameter increment for the sample trees. This model can take on many forms and can be integrated to obtain cumulative diameters. Typically, the increment form of the Chapman-Richards curve is a function of cumulative size so that time is included implicitly in the function. This can cause statistical problems in modelling because the increment and diameter are autocorrelated (Gertner 1981). However, the diameter increment (D_{inc}) function can be obtained as a function of time by differentiating the cumulative form of the model with respect to time,

[9] $D_{inc} = k\, D_{\infty}\{1 - \exp[-k(t-t_0)]\}^{m/(1-m)}\exp[-k(t-t_0)]/(1-m)$,

with parameters m, k, D_{∞}, and t_0.

After examining the Type 2 sequences for each section and the three-dimensional diameter increment-height-age surfaces, the following system of equations was proposed. Each Type 2 sequence can be characterized by the increment form of the Chapman-Richards function [9], with parameters m, k, D_{∞}, and t_0 which depend on height along the stem. Derivation of a

continuous function for diameter increment follows the general model described earlier, equations [1] to [8]. The parameter t_0 from [9] is the age at which the tree reaches total height H, and is given by the inverse of the height-age curve. The ring count for each section is $(t - t_0)$, and no diameter increment occurs at height h when $t \leq t_0$. The cumulative version of the Chapman-Richards function,

[10] $H = H_\infty\{1-\exp[-k't_0]\}^{1/(1-m')}$,

with parameters H_∞, k', and m', was used to fit the height-age data. H_∞ is the asymptotic height the tree will approach as t_0 becomes large. The inverse of [10] was used to obtain t_0,

[11] $t_0 = -\ln[1 - (H/H_\infty)^{1-m'}]/k'$.

The parameter t_0 from [9] can be expressed as a function of height along the stem (h) using [11] with H = h.

The other parameters of the Chapman-Richards function or functions of them can also be used to develop a continuous model for D_{inc} over all heights. The parameter D_∞ is the asymptotic diameter at height h, the diameter the tree will eventually approach at that height. Using the asymptotic height, H_∞, estimated with [10], one can develop an asymptotic taper equation based on the inverse of the Chapman-Richards function (refer to Appendix B),

[12] $D_\infty = D_\infty(.3)\{1 + a \ln[1-(1-\exp(-1/a))((h-.3)/(H_\infty-.3))^{1/b}]\}$,

where $D_\infty(.3)$ is the asymptotic diameter obtained from [9] for the stump section (0.3 m), and a and b are parameters to be estimated. Biging (1984) used the inverse of the Chapman-Richards function to develop taper equations for conifers in

northern California. The main difference between [12] and Biging's (1984) model is that [12] is constrained to equal $D_\infty(.3)$ at h equal 0.3 m, while Biging's (1984) model is constrained to go through DBH. Additionally, [12] requires only two parameters. The model is constrained to equal zero when h equals H_∞.

One can obtain $D_{inc\ max}$ and t_{max} for each height from the parameters D_∞, m, k, and t_0. One can obtain t_{max} by differentiating [9] with respect to t, setting this equal to zero, and solving for t_{max},

[13] $t_{max} = t_0 - [\ln(1-m)]/k.$

$D_{inc\ max}$ is obtained by substituting t_{max} into [9],

[14] $D_{inc\ max} = D_\infty\ k\ m^{m/(1-m)}.$

As discussed in Chapter one, $D_{inc\ max}$ increases and then decreases with increasing height along the stem. Also, with increasing height, t_{max} tends to approach t_0, so that as the tree gets older the maximum diameter increment tends to occur at an earlier ring count. Using these relationships, both $D_{inc\ max}$ and t_{max} can be modelled as functions of height. If t_0 is given by [11] and D_∞ is given by [12], this forms a system of two equations with two unknowns, m and k,

[15] $t_{max} = t_0 - [\ln(1-m)]/k = f(\underline{a},h),$

[16] $D_{inc\ max} = D_\infty\ k\ m^{m/(1-m)} = g(\underline{\gamma},h),$

which could be simultaneously solved to obtain the two parameters as functions of height along the stem. However, both [15] and [16] are nonlinear equations with regard to m and k, so that explicit solutions cannot be obtained. An alternative

approach is to estimate m as an exponentially declining function of height, since m is the relative position at which the maximum increment occurs (Pienaar and Turnbull 1973). A negative exponential function with parameters c and d was suggested to model m as a function of height,

[17] $m = c \exp(d(h))$.

A tentative model for $g(\chi,h)$ was the increment form of the Chapman-Richards function,

[18] $D_{inc\ max} = k"A\{1-\exp[-k"h]\}^{m"/(1-m")} \exp[-k"h]/(1-m")$,

with parameters A, k", and m". Modelling $D_{inc\ max}$, m, and D_∞ as a functions of height, [16] can be used to arrive at a constrained function for k.

PARAMETER ESTIMATION

Nonlinear regression was used to obtain maximum likelihood estimates of the parameters using a quasi-Newton algorithm (White 1978). Model [10] was used to fit the height-age data for each tree. Because periodic rather than annual measurements of height were used there should be no problem with using the cumulative version of the Chapman-Richards function to obtain parameter estimates (Gertner 1985). The parameter estimates from [10] were used in [11] to predict values of t_0 at various heights. The parameter H_∞ was used in determining second-stage estimates of D_∞ and k.

Parameter estimation for the other models was done in two stages. First-stage estimates of m, k, and D_∞ were obtained for

each section from the five trees. These estimates or functions of them were then modelled as functions of height in the second stage of estimation. Although, the second-stage parameter estimates are inefficient, they are still unbiased (Kmenta 1971). Estimates from all sections on all trees were pooled together for the second-stage of estimation. Using first-stage estimates of D_∞ at the stump ($D_\infty(.3)$) and estimates of H_∞ from each tree, second-stage estimates of D_∞ were obtained using [12] (Fig 2.1). Plots of m against height (Fig. 2.2) indicated [17] was appropriate for the second-stage model form to predict m. Plots of $D_{inc\ max}$ versus height (Fig. 2.3) indicated that the [18] would be suitable to predict $D_{inc\ max}$. Substituting [12], [17], and [18] into [16] and solving for k, a constrained function for k was obtained. With this system of equations to predict m, k, D_∞, H, and t_0, diameter increment along the stem can be determined for any age.

RESULTS AND DISCUSSION

Substituting the models to predict m, k, D_∞, and t_0 (Table 2.1) as functions of height into [9], diameter increment can be estimated for any age and height along the stem of an individual tree (Fig 2.4). The Type 1 sequences from the simulated diameter increment follow the pattern of the observed surface (Fig 2.4). There is an increase in diameter increment toward the base of the tree which does not occur in previous models (Arney 1972, 1974; Mitchell 1975). In addition, the simulated

Type 1 sequences tend to flatten out as the tree becomes older, a feature consistent with the observed data.

A model for taper can be obtained by substituting the models that predict m, k, D_∞, and t_0 into the cumulative form of the Chapman-Richards function. Because the model depends on age and height along the stem, changes in stem form are predicted over time (Fig. 2.5). The model allows changes in upper stem diameters that may not be predicted by just taking into account the change in DBH. Eventually the tree will approach the form given by [12], the asymptotic taper. The model also predicts the development of butt swell as the tree becomes older. However, the predicted taper of the tree towards the tip in later years tends to flatten out, which may be due to the form of the asymptotic taper model.

Volumes at different ages were determined by numerical integration using a closed Newton-Cotes formula of order 4 (Burden et al. 1981) and compared to actual volumes (Fig 2.6). The simulated volumes follow a sigmoid growth curve, and the predictions agree fairly well with the observed volumes up to about 100 years. The model tends to underestimate volumes beyond this time. This is probably due to a continuing decrease in predicted diameter increments at lower heights, while the observed Type 2 series tend to level off to a near constant value, resulting in underestimation of lower diameters at later ages. The limit of [9] as t becomes large is zero, so that the diameter increment model is approaching zero too quickly. The model could be constrained to approach a higher limit as t

becomes large. However, since the diameter increment appears to reach a constant value, cumulative diameters are still increasing and the use of a function with an upper aysmptote may be questionable. Given the general modelling framework outlined earlier, other models can be examined.

If confidence intervals are to be used or differences in parameters are to be tested, future work should examine ways to obtain efficient parameter estimates. First-stage estimates of m, k, and D_∞ were obtained from individual regressions for each section. If there is a disturbance at some point in time, it may affect growth at several heights along the stem, so that errors for the models at different heights will be correlated. Because, it is likely that there is cross-equation correlation of error terms, more efficient estimates of these parameters can be obtained by using SUR (Seemingly Unrelated Regressions) procedure (Kmenta 1971). Because diameter increments tend be autocorrelated with previous diameter increments, this correlation within a model also should be taken into account. Likewise, the variance of diameter increment appears to decrease with increasing time. In order to obtain efficient estimates of these first-stage parameters, cross-equation correlation of errors, autocorrelation of errors within an equation, and non-constant variance of the errors for each equation should be taken into account in order to obtain efficient first-stage parameter estimates. Because the parameters from the first stage are not estimated without error, and the error terms from each of the second-stage models may be correlated, the second-

stage parameter estimates may also not be efficient since each second-stage model was estimated separate from the others. Correcting these problems may be quite difficult because of the nonlinear models and lack of computer software to find parameter estimates.

A new method has been presented to model diameter increment along the stem and obtain compatible estimates of diameter increment, taper, and volume that can be included as a component in growth and yield models. The model provides diameter increment estimates that are consistent with the Duff and Nolan Type 1 and 2 sequences, despite some slight biases in predictions of volume, taper, and diameter increment at ages beyond 100 years. The influences of competition and crown development are not included in the model, but could be incorporated using the approach of Arney (1972) if data on density and crown characteristics were available. One model appears to accurately predict changes in stem diameter increments for the five trees examined. Additional work needs to be done to examine site and density effects, and how silvicultural treatments such as thinning and fertilization affect diameter increment along the stem over time and modify the functions to account for these effects.

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Table 2.1 Overall parameter estimates for final models.

Parameter	Parameter estimate	Used in equation in text
H_∞	19.2351	[10] [11] [12]
k'	0.0171	[10] [11]
m'	0.1433	[10] [11]
a	0.2129	[12]
b	6.5057	[12]
$D_\infty(.3)$	306.0600	[12]
c	0.2601	[17]
d	-0.1546	[17]
k"	0.0696	[18]
A	112.8667	[18]
m"	0.1009	[18]

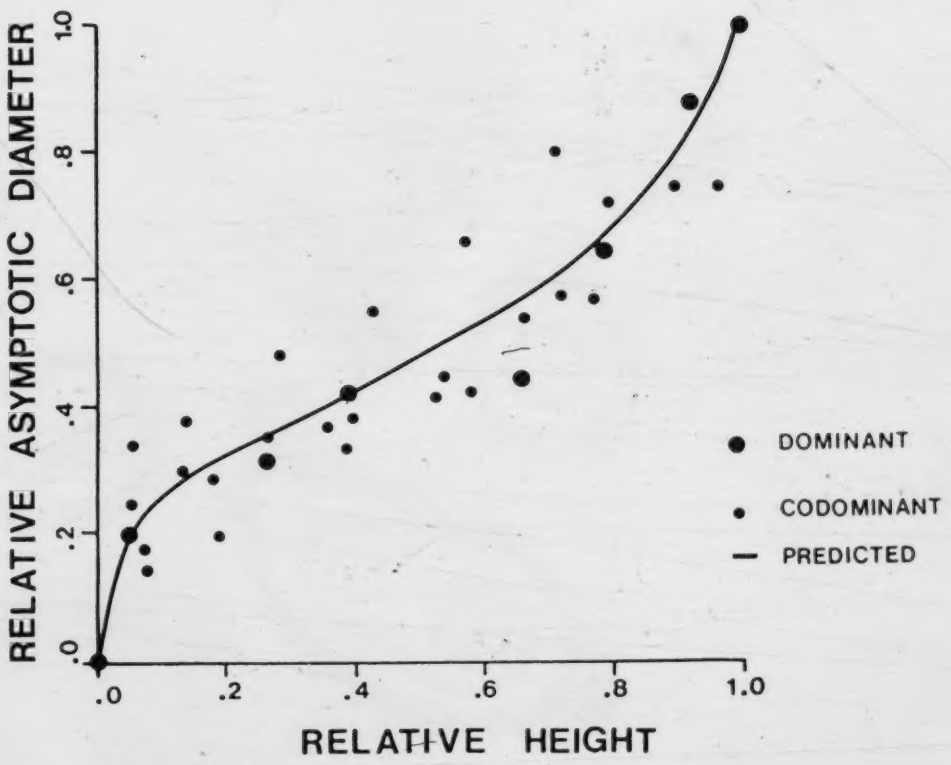

Figure 2.1. First-stage and second-stage estimates of relative D_∞ (asymptotic taper) plotted against relative height. Relative $D_\infty = 1 - D_\infty/D_\infty(0.3)$ and relative height = $(h-.3)/(H_\infty-.3)$.

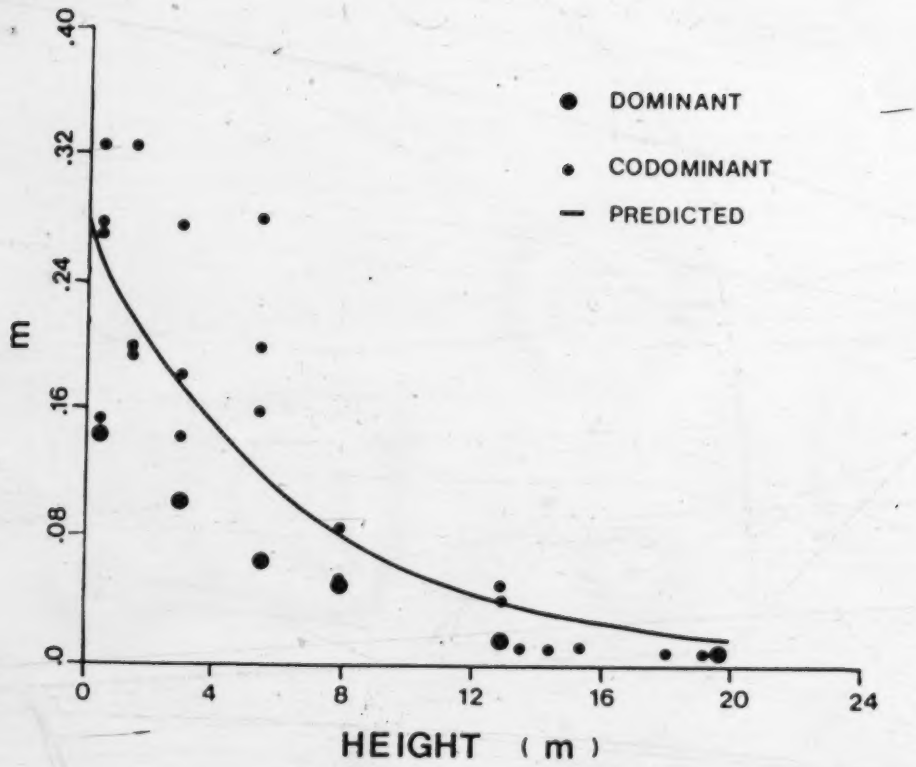

Figure 2.2. First-stage and second-stage estimates of m plotted against height.

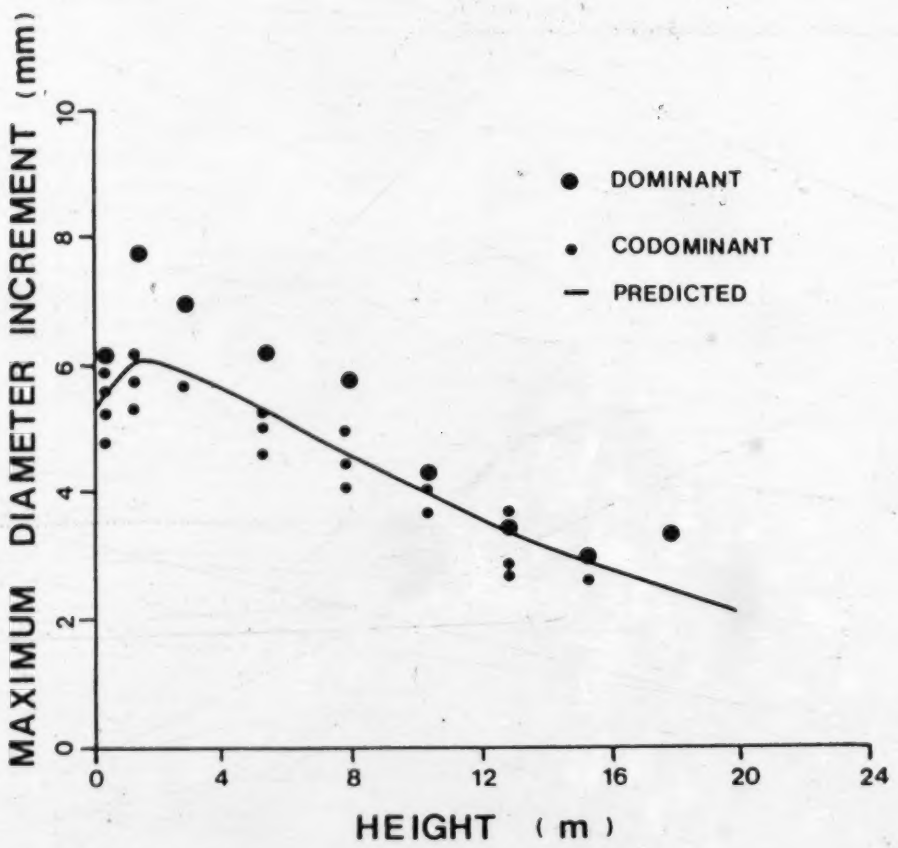

Figure 2.3. $D_{inc\ max}$ and predicted $D_{inc\ max}$ plotted against height.

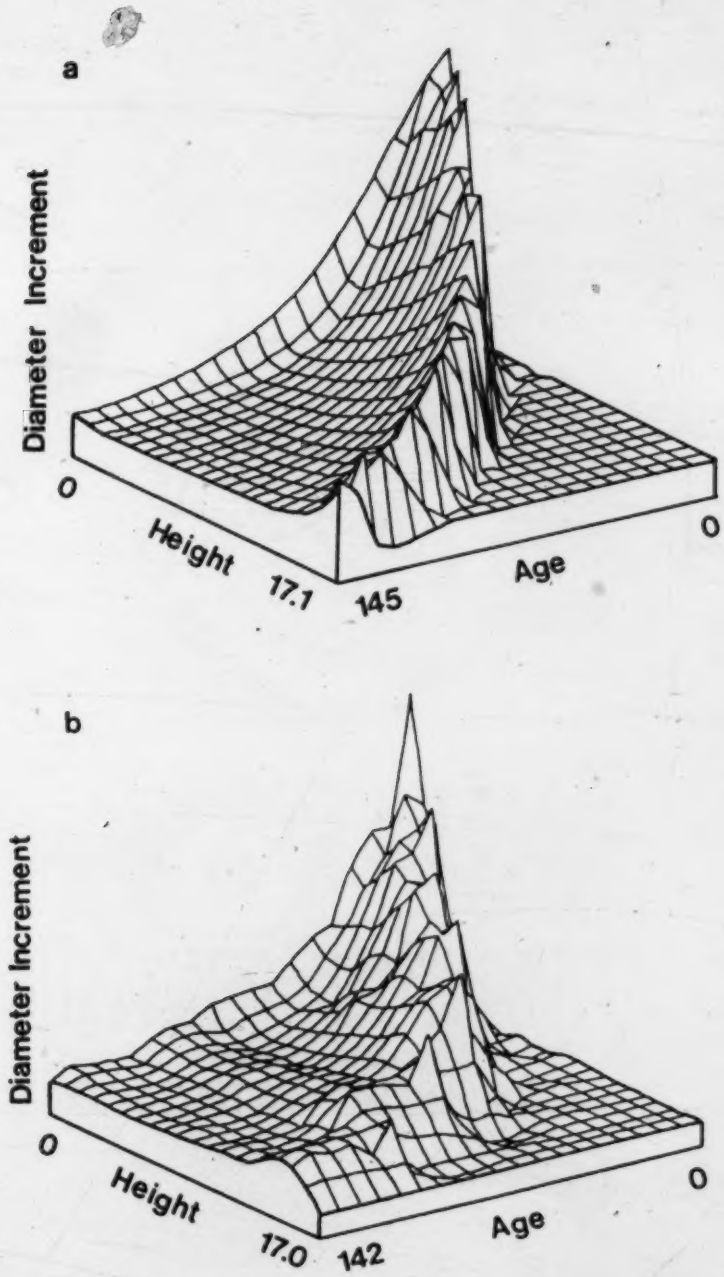

Figure 2.4. Predicted (a) and observed (b) diameter increment surfaces for various ages and heights along the stem for a codominant lodgepole pine.

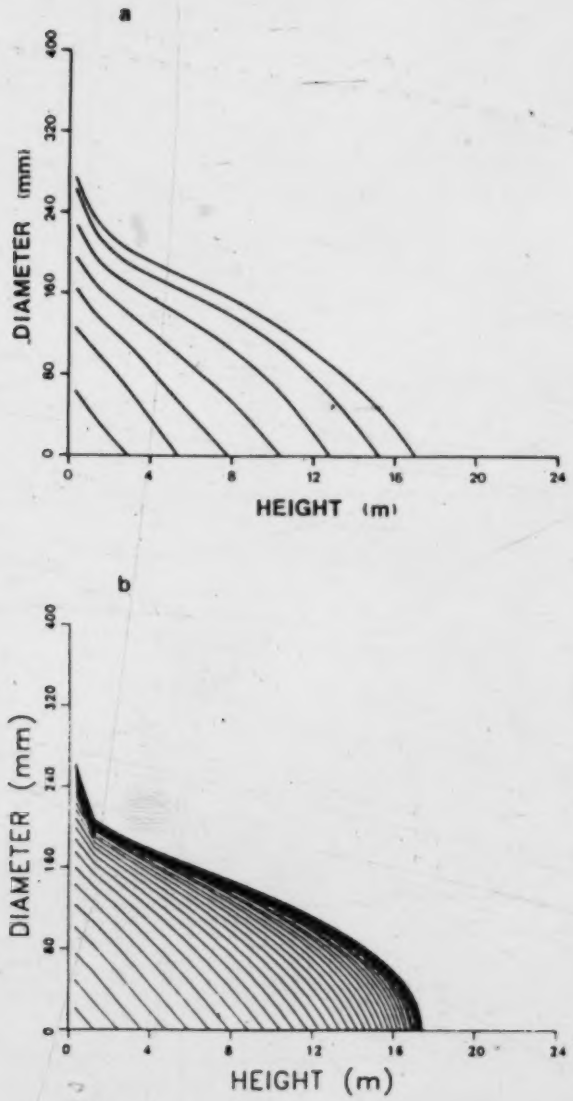

Figure 2.5. Observed (a) and simulated (b) taper for a codominant lodgepole pine at different age intervals.

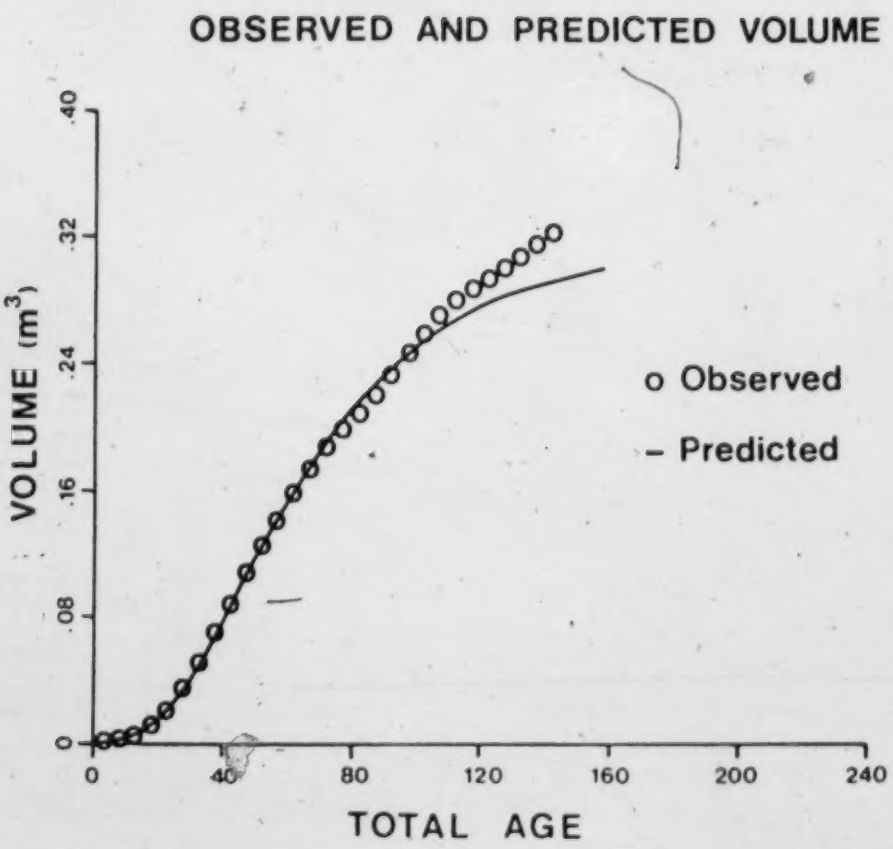

Figure 2.6. Observed and simulated total stem volumes for a codominant lodgepole pine.

HOW REASONABLE ARE TAPER EQUATIONS FOR PREDICTING CHANGES IN STEM DIAMETERS?

INTRODUCTION

Taper equations can provide accurate predictions of diameters at various heights along the stem, and can be integrated to obtain volume estimates of any portion of the stem (Kozak et al. 1969). Most taper models assume a single form for all individuals in a population (Kozak et al. 1969; Demaerschalk 1973; Ormerod 1973; Goulding and Murray 1976; Max and Burkhart 1976; Demaerschalk and Kozak 1977; Bennet et al. 1978; Amidon 1984; Biging 1984), although recent studies have incorporated crown ratio into the models to allow the stem profile to change as crown ratio changes (Dell 1979; Feduccia et al. 1979; Burkhart and Walton 1985; Walters and Hann 1986). Newberry and Burkhart (1986) developed a variable-form stem profile model that allowed the parameters of Ormerod's (1973) model to change as functions of diameter at breast height (DBH), crown ratio, age, and site index.

When a taper model is used as a component of an individual-tree growth and yield model, usually only DBH and total height are projected to obtain future stem diameters and volume (Arney 1985). However, the change in DBH over time may not accurately reflect the change in diameters at other positions along the stem. There have been few quantitative studies examining variation in stem diameter growth and how this relates to stem

taper (Arney 1972,/1974; Mitchell 1975). However, even these attempts did not actually include measurements of stem diameter increments over time. When used in growth projection, it would be ideal if taper models predicted diameter increment along the bole consistent with observed patterns of diameter increment. Unfortunately, most taper equations are empirical models with little biological basis. These equations are based on cumulative diameters and heights rather than the diameter increments which represent the underlying growth processes. The objective of this study is to determine how well some of the current taper equations implicitly describe diameter increment along the stem over time. Diameter increment models are obtained as the first derivative of the taper functions and predictions using these increment models are compared to the observed surface of diameter increment at various ages and heights along the stem for selected individual trees.

DERIVATION OF A STEM DIAMETER INCREMENT MODEL

Clutter (1963) derived a growth function by taking the first derivative of a yield function, so that estimates of growth would be consistent with yield predictions. A diameter increment function can be obtained directly from a taper equation by differentiating the taper function with respect to time. Throughout this paper, D will refer to diameter at any height along the stem, while DBH will refer to diameter at breast height. Let $D = z(DBH,H,h)$ be any taper equation with

continuous partial derivatives, where h is height along the stem and H is total height. If H = f(t) and DBH = g(t) are any two differentiable functions of time (t), then D is a differentiable function of t. The change in diameter with respect to the change in time (dD/dt) can be obtained by the chain rule for partial derivatives, and is given by,

[1] $dD/dt = (\partial D/\partial DBH)(dDBH/dt) + (\partial D/\partial H)(dH/dt)$,

which is approximately,

[2] $\Delta D/\Delta t = (\partial D/\partial DBH)(dDBH/dt) + (\partial D/\partial H)(dH/dt)$,

with a remainder or error term given by a second order Taylor's expansion,

[3] $R(t) = 0.5[(\partial^2 D/\partial DBH^2)(dDBH/dt)^2 + (\partial D/\partial DBH)(d^2DBH/dt^2) + 2(\partial^2 D/\partial DBH\partial H)(dDBH/dt)(dH/dt) + (\partial^2 D/\partial H^2)(dH/dt)^2 + (\partial D/\partial H)(d^2H/dt^2)]\ (\Delta t)^2$, evaluated at $t = \xi$,

where $\Delta t = t_1 - t_0$, and $t_0 \leq \xi \leq t_1$ (Gillett 1981). The error in using [2] to approximate [1] will be $\leq$ maximum of $|R(\xi)|$. Equation [2] can be used to determine the diameter increment (ΔD) for some time interval for a given taper equation.

MATERIALS AND METHODS

Stem analysis disks were obtained from the Alberta Forest Service for 36 lodgepole pine (Pinus contorta var. latifolia Engelm.; 11 dominants, 22 codominants, 3 intermediates) trees located in three stands east of Grande Cache and eight stands south of Grande Prairie, Alberta. All plots were in mixed-wood stands consisting of lodgepole pine, white spruce (Picea glauca

[Moench] Voss), black spruce (Picea mariana [Mill.] B.S.P.), and balsam fir (Abies balsamea [L.] Mill.), with a minor component (less than 20 percent of stand volume) of aspen (Populus tremuloides Michx.). Site conditions ranged from fair to good, with seven of the eleven plots sampled classified as medium site (Alberta Energy and Natural Resources 1985).

Sections were removed at the stump (0.3 m), breast height (1.3 m), and at 2.5 m intervals above the stump. The number of annual rings was determined for each section, and annual radial increments were measured to the nearest 0.01 mm along the longest and shortest axes using a computerized tree ring measuring device (Appendix A). Annual diameter increment was calculated as twice the arithmetic mean of the four radial increments, and the diameter for that year obtained as the sum of the previous diameter increments.

From stem analysis data, it is possible to reconstruct previous taper profiles of a tree. Although this procedure results in diameters that are not independent from previous diameters, the number of years between diameters in this study tended to be far enough apart to reduce problems with autocorrelation between diameters in different measurement periods at the same height (Gertner 1985). In this study, only obtaining parameter estimates for each taper model is of interest. If autocorrelation between diameters in different measurement periods at the same height does exist, the parameter estimates from ordinary least squares regression will still be unbiased, although inefficient (Draper and Smith 1982). Only

data for years in which the total tree height was known (where a section was taken), and for which there were at least four sections, were used for analysis. The remainder of the diameter increment data was used for validation. Data were pooled for all ages and trees (1056 observations) so that the data set was representative of the size classes normally used to develop taper equations.

Parameters were estimated for four taper equations (Table 3.1) using ordinary least squares regression or nonlinear regression where appropriate. Parameters were estimated using the model forms presented by the various authors (Table 3.1). Both the Max and Burkhart (1976) and Kozak et al. (1969) use squared relative diameter as the dependent variable. D was obtained by rearranging the models to determine the derivatives. Both DBH and height were estimated as functions of age for each tree using the Chapman-Richards growth curve (Pienaar and Turnbull 1973),

[5] $\Delta DBH = k\, D_\infty\{1 - \exp[-k(t-t_0)]\}^{m/(1-m)}\exp[-k(t-t_0)]/(1-m)$,

[6] $DBH = D_\infty\{1-\exp[-k(t-t_0)]\}^{1/(1-m)}$,

[7] $\Delta H = k'\, H_\infty\{1 - \exp[-k't]\}^{m'/(1-m')}\exp[-k't]/(1-m')$,

[8] $H = H_\infty\{1-\exp[-k't]\}^{1/(1-m')}$,

with parameters k, m, D_∞, k', m' and H_∞. Because annual measurements were available for diameter increment, parameters m, k, and D_∞ were estimated using [5] (Gertner 1981). Since height measurements were taken at intervals of 2.5 m, [8] was the functional form used to obtain estimates of m', k' and H_∞. The parameter t_0, the number of years it takes the tree to reach

1.3 m was obtained by solving [8] for t_0. The parameter estimates from the taper equations (Table 3.1), and predicted values from [5], [6], [7], and [8] were used in the diameter increment functions for each taper model (Table 3.2) to obtain annual diameter increments at various ages and heights along the stem. The diameter increments were plotted against height and age, and compared to the observed diameter increment surface for a subset of the data (10 trees) (Fig. 3.1).

RESULTS AND DISCUSSION

The models varied in their ability to predict taper and stem diameter increment over time. Both the Kozak et al. (1969) and Amidon (1984) models are based on a quadratic function of height. A simple quadratic function is not able to adequately describe the the butt swell (Cao et al. 1980) or predict an increase in diameter increment near the base of the tree (Fig. 3.1). In order to account for the butt swell, segmented taper models, such as those of Max and Burkhart (1976) and Bennet et al. (1978), can be used. Max and Burkhart's (1976) taper model is based on three quadratic functions, with each quadratic based on the model of Kozak et al. (1969). The taper model of Bennet et al. (1978) is based on two segments joined at breast height. Both segmented models predict an increase in diameter increment toward the base of the tree.

While the form of the predicted diameter increment surfaces appear very similar to the observed surface (Fig 3.1), there are

some differences. Duff and Nolan (1953, 1957) described the Type 1 sequence as variation in diameter increment along the stem for one age. The Type 1 sequence can be seen in Fig. 3.1 by following the lines on the surface drawn parallel to the height axis. This sequence decreases from the base to a minimum and then increases toward the tip of the tree. In young trees, there is a strong increase in diameter increment near the top. As the tree ages, the sequence flattens out over most of the bole, with an increase in diameter increment near the base and only a slight increase toward the tip. The increase of diameter increment near the base over several years results in the development of butt swell. As mentioned above, models that are not capable of predicting the increase in diameter increment toward the base the tree are also unable to predict the resulting butt swell. Amidon's (1984) model also does not predict an increase in diameter increment along the stem. The Type 1 sequence predicted by Amidon's model remains relatively flat for all ages. The Type 1 sequence predicted by the model of Kozak et al. (1969) does only slightly better, predicting a sharp increase in diameter increment close to the tip, but otherwise remaining fairly constant over most of the bole.

The taper models of Bennet et al. (1978) and Max and Burkhart (1976) predict a more reasonable pattern of diameter increment for the Type 1 sequences. Both models predict an increase in diameter increment near the base of the tree. However, both models predict a greater difference between increment near the base and the section above at a younger age.

As the tree ages, the models predict the difference between increment near the base and the section above will decrease, or the slope of the Type 1 sequence near the base becomes flatter with increasing age. In contrast, the observed difference between diameter increment near the base and the section above remains constant over time or may increase slightly.

Duff and Nolan (1953, 1957) described the radial sequence in diameter increment as a Type 2 sequence. The Type 2 sequence can be seen by following the lines parallel to the age axis in Fig. 3.1. For sections near the base of the tree, the sequence increases rapidly from the center of the tree, reaches a maximum diameter increment and then decreases with increasing age. The number of rings from the center of the tree to the maximum diameter increment for each section declines with increasing height along the stem, until eventually the Type 2 sequences start off at the maximum diameter increment and then continue to decline with increasing age. The maximum diameter increments for each section also display a regular pattern of variation in a progression up the stem. Starting at the base, the largest diameter increment at each height increases to some maximum value and then declines with increasing height. Thus, the largest diameter increment value does not necessarily occur at the base or at breast height.

Few of the Type 2 sequences predicted by the various taper models were consistent with the observed sequences. In all models, the predicted Type 2 sequences reach a maximum increment much earlier than in the observed sequences. For most of the

trees, the maximum diameter increment for each predicted Type 2 sequence was greatest at the base of the tree and declined with increasing height, rather than increasing to a maximum value and then declining as in the observed sequences.

Since the diameter increment surface varies with tree and stand conditions (refer to Chapter 1), taper models which allow the stem form to change under different growing conditions (Newberry and Burkhart 1986) may be better able to predict diameter increment along the stem over time that is more consistent with the observed patterns of variation. In general, the form of the diameter increment surface predicted from the various models is fairly similar to the observed values. Results from this study indicate that segmented models predict Type 1 sequences that are more consistent with the observed sequences, and are better at predicting the increase in diameter increment toward the base of the tree. There were some inconsistencies between the observed and predicted Type 2 sequences for all of the taper models examined. It appears that to obtain predictions of diameter increment along the stem over time that are consistent with the growth and development of a tree, variables other than DBH and height increment or more complex models must be considered.

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Table 3.1. Four taper equations examined in this study.

Max and Burkhart (1976)

$$D^2/DBH^2 = b_1(h/H - 1) + b_2(h^2/H^2 - 1) + b_3(a_1 - h/H)^2 I_1 + b_4(a_2 - h/H)^2 I_2$$

$$I_i = \begin{cases} 1 & \text{if } h/H < a_i \\ 0 & \text{if } h/H \geq a_i \end{cases} \qquad i = 1, 2$$

Kozak et al. (1969)

$$D^2/DBH^2 = b_1(h/H - 1) + b_2(h^2/H^2 - 1)$$

Bennet et al. (1978)

$$D = DBH(h/1.3)^{b_0} \qquad \text{if } 0.3 \leq h \leq 1.3 \text{ otherwise}$$

$$D = DBH[(H - h)/(H - 1.3)] + b_1(H - h)(h - 1.3)/H^2 + b_2 DBH(H - h)(h - 1.3)/H^2 + b_3 DBH^2(H - h)(h - 1.3)/H^2 + b_4(H - h)(h - 1.3)(2H - h - 1.3)/H^3$$

Amidon (1984)

$$D = b_1 DBH(H - h)/(H - 1.3) + b_2(H^2 - h^2)(h - 1.3)/H^2$$

D diameter inside bark at any point along the stem at height h

DBH diameter inside bark at breast height (1.3 m)

h height above the ground to diameter D

H total height of the tree

a_i estimated join points

b_i estimated regression coefficients

Table 3.2. Annual diameter increment functions derived from four standard taper equations.[a]

$$\Delta D = (\partial D/\partial DBH)\Delta DBH + (\partial D/\partial H)\Delta H$$

Max and Burkhart

$$\partial D/\partial DBH = [b_1(h/H - 1) + b_2(h^2/H^2 - 1) + b_3(a_1 - h/H)^2 I_1 + b_4(a_2 - h/H)^2 I_2]^{1/2}$$

$$\partial D/\partial H = 0.5(DBH)(\partial D/\partial DBH)^{-1}(-h/H^2)\{b_1 + 2[b_2(h/H + b_3 I_1(h/H - a_1) + b_4 I_2(h/H - a_2)]\}$$

Kozak et al.

$$\partial D/\partial DBH = [b_1(h/H - 1) + b_2((h/H)^2 - 1)]^{1/2}$$

$$\partial D/\partial H = .5(DBH)(\partial D/\partial DBH)^{-1}(-h/H^2)[b_1 + 2b_2(h/H)]$$

Bennet et al.

$$\partial D/\partial DBH = (h/1.3)^{b_0} \quad \text{if } 0.3 \leq h \leq 1.3 \text{ otherwise}$$

$$\partial D/\partial DBH = (H-h)/(H-1.3) + b_2(H-h)(h-1.3)/H^2 + 2(DBH)b_3(H-h)(h-1.3)/H^2$$

$$\partial D/\partial H = b_0(1.3)^{b_0}(DBH)\,H^{(b_0-1)} \quad \text{if } 0.3 \leq h \leq 1.3 \text{ otherwise}$$

$$\partial D/\partial H = [1 - (H-h)/(H-1.3)]/(H-1.3) + b_2(DBH)(h-1.3)[1 - 2(H-h)/H]/H + b_3(DBH^2(h-1.3)[1 - 2(H-h)/H]/H + b_4(h-1.3)[(4H-3h-1.3) - 3(H-h)(2H-h-1.3)/H]/H^3$$

Amidon

$$\partial D/\partial DBH = b_1(H-h)/(H-1.3)$$

$$\partial D/\partial H = b_1(DBH)[1 - (H-h)/(H-1.3)]/(H-1.3) + 2b_2(h-1.3)[1-(H^2-h)/H^2]$$

[a] Equations for DBH, ΔDBH, H, and ΔH are given in the text.

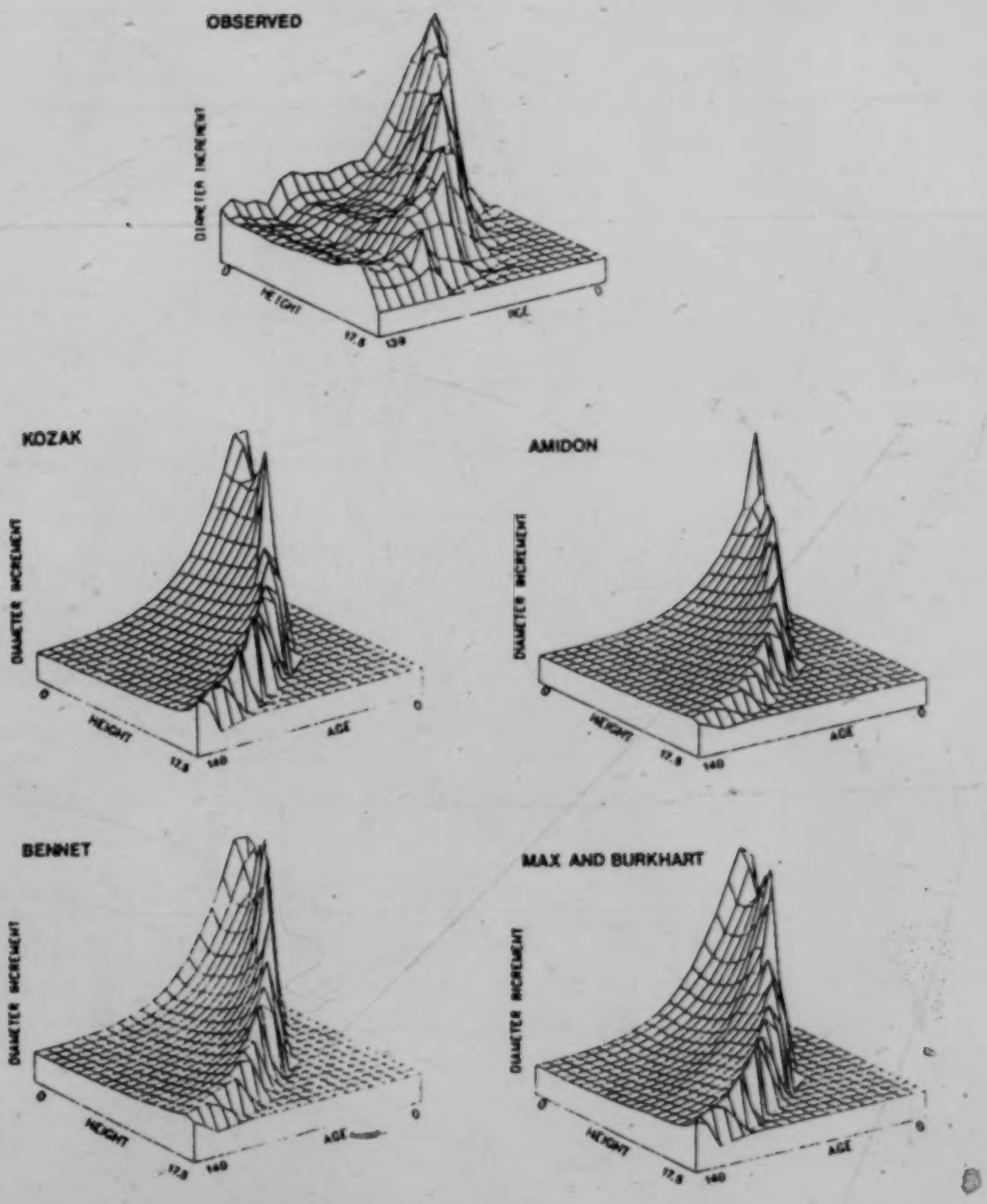

Figure 3.1. Observed and predicted diameter increment as a function of height along the stem and age for various taper models.

GENERAL CONCLUSIONS

This study has examined several aspects of changes in diameter increment with height along the stem and age within individual trees for lodgepole pine, white spruce, and black spruce in Alberta. The first chapter demonstrated that diameter increment changes over time at different rates depending on the height along the stem. The pattern of variation in diameter increment differed among species and among crown classes within species. The differences among species may be partly explained by their relative shade tolerance, with more tolerant species being able to maintain a more consistent level of diameter increment over a longer period of time. In lodgepole pine, a shade intolerant, early seral species, diameter increment rapidly declines after reaching an early peak. This is likely due to the species' inability to maintain a high level of diameter growth after crown closure. In contrast, the shade tolerant spruces are able to maintain a relatively higher level of diameter growth even when shaded by adjacent crowns. It is expected that in more open stands the maximum diameter increment at a given height will occur later than in more dense stands. Shading may also explain differences among crown classes. Because the crowns of dominant trees extend above the general level of the canopy and receive light from above and the sides, they are better able to maintain diameter growth closer to the peak levels at positions along the stem. The crowns of codominants form the general level of the canopy and growth

rates drop off at a more rapid rate than in dominants, as they are getting direct light only from above. Because the crowns of intermediate trees are within the canopy and receive even less light, diameter increment drops off rapidly after reaching a peak at each height. These differences in diameter increment are reflected in the resulting stem form.

In the second chapter, a model was developed for diameter increment based on the observed patterns of variation with height and age discussed in the first chapter. This model uses the increment form of the Chapman-Richards growth curve to characterize the distribution of diameter increment over time for each height. The parameters of these growth curves were modelled for each section as functions of height to obtain a model to predict diameter increment over a continuous range of ages and heights along the stem. Predicted stem profiles and volumes obtained from this model were consistent with observed growth data for five lodgepole pine trees. Although volumes were under-predicted beyond 100 years, the predictions follow a sigmoid growth curve, as expected.

Because taper models implicitly define a relationship for stem diameter increment when used with DBH and height growth models, the third chapter addressed the question of how reasonable this method is for predicting diameter increment along the stem over time. The four standard taper models examined did not accurately reflect observed differences in diameter growth rates at different positions along the stem. Segmented models were better at predicting changes in diameter

increment at various heights over time. Although predictions made using these models are reasonable, it appears that variables other than DBH and height growth must be included or other functional relationships must be used if consistent estimates of diameter increment are desired.

Because density and the crown characteristics influence the distribution of diameter increment along the stem, a better understanding of diameter growth along the stem over time could be obtained by including measurements of these variables over time. This could be done by combining permanent sample plot data and stem analysis measurements. Also, stem analysis sections taken at every internode along the stem rather than at 2.5 m intervals would provide more information on diameter and height growth, and the relationship between them, so a more precise model for diameter increment could be developed. However, taking measurements closer together may result in greater problems with autocorrelation between successive data points. More efficient estimation procedures can also be used to obtain parameter estimates so that confidence intervals or hypothesis testing can be done. Models other than the Chapman-Richards function can be investigated to determine whether they provide better estimates of diameter increment beyond 100 years. Measures of site quality, density, crown class, and crown development should also be included as variables in future models for diameter increment.

APPENDIX A

A NEW COMPUTERIZED SYSTEM FOR TREE RING MEASUREMENT AND ANALYSIS[1]

INTRODUCTION

Accurate measurement of diameter increment from stem analysis or increment cores is important for reconstructing the past growth and development of a tree for dendrochronology and growth and yield studies. Undertaking such a task manually is quite time consuming and can result in errors at several stages in the measurement process. By using a computerized system for measuring diameter increment, data recording and keypunching errors can be eliminated, and measurement accuracy and precision can be improved.

In currently available automated systems, such as the Addo-X or Digi-Mic, examination and analysis of data are not easily done during the measuring stage. (See Bains and Micko [1985] for a comparison of the two systems.) This lag between data measurement and editing makes error detection and correction more difficult. The Tree Ring Measurement System was designed to overcome some of the shortcomings of existing measurement

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[1] A version of this appendix has been submitted for publication to the Forestry Chronicle by M. A. Clyde and S.J. Titus.

systems. It is relatively inexpensive compared to other automated systems, allows data to be displayed, plotted, or measured at any time from within the program, and is quite flexible, allowing other options to be added to the system by modifying the software.

DESCRIPTION OF SYSTEM

The Tree Ring Measurement System consists of a boom binocular microscope, positioning mechanism, and an IBM PC/XT/AT microcomputer system (Fig. 1). Minimum configuration of the microcomputer requires two disk drives, 512K memory and a math-coprocessor. The positioning mechanism controls movement of the core or disk under the microscope and can be fit with a platter for disks or an increment core holder, mounted on a swivel base to compensate for the orientation of each growth ring.

The microcomputer is interfaced to a BEI optical incremental encoder[2] which is coupled to the base of the positioning mechanism by a rack and anti-backlash gear. Incremental analog-to-digital encoders are devices for measuring movement of a mechanical input. Rotation of the shaft of the optical encoder by turning the thumb-wheel causes a sensing of motion and direction, with output in the form of digital voltage levels.

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[2] The BEI LED optical encoder model 5VL79D-4 is available from BEI Electronics, Inc., 1101 McAlmont, P.O. Box 3838, Little Rock, Arkansas, USA 72203 Phone: (501) 372-7351.

Since the direction is indicated electronically by the optical encoder, the computer circuitry can count the pulses in either direction with an up-down counter[3]. The accumulated "counts" can then be translated into the distance the sample has moved.

ACCURACY

Because the distance is determined from electronic pulses, and the counter is incremented only after a complete pulse is generated, a small measurement error results from the computer's inability to count a fraction of a pulse. The counter is reset after every measurement so that errors do not accumulate, limiting the maximum error associated with each measurement to the distance per count. A Linear Variable Differential Transformer (LVDT) was used for calibrating and empirically determining the accuracy of the system (Herceg 1976). LVDT's are very accurate instruments for electronic measurement of displacement of an object. The LVDT used for calibration was approximately three times as accurate as the optical encoder. The optical encoder outputs one pulse per 0.00746 $\pm$ 0.000230 mm,

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[3] A microcomputer board could not be obtained commercially with an up-down counter and 5-volt power supply for the optical encoder. The up-down counter board was built by Technical Services at the University of Alberta. Schematic diagrams of the board and positioning mechanism are available from the authors.

based on 50 repeated calibration trials (values are mean ± one standard deviation). Because the maximum error of the encoder will be less than the distance associated with one count, the maximum absolute error will be constant for all distances measured. However, as the distance measured increases, the maximum relative error will decrease. On average, the maximum relative error for a 0.1 mm distance would be less than 7.5 percent. For distances greater than 1.0 mm, the maximum relative will be less than 0.75 percent. On average, the error will be smaller, as evidenced by the value of the standard deviation, which includes the error associated with the optical encoder and any mechanical errors in the system. The Digi-Mic and Addo-X are reported to be accurate to 0.01 mm.

SOFTWARE FEATURES

Unlike other measurement systems, measurement control originates with the microcomputer's software. The program is written in IBM Professional Fortran, with Fortran callable Assembly Language subroutines for reading distances from the counter, since Fortran does not have the facilities to read from input ports. All commands are displayed in a menu with options selected by pressing the appropriate function key or as a prompt with input from the keyboard.

The operator can specify the direction of measurement, either from center to bark, or from bark to center. During data acquisition, radial growth increments and corresponding ages are

displayed on the screen. The program allows measurement of a maximum of four radii per section, and will test whether ages of all radii in a section are equal. If the different radii in a section do not have the same age, the complete radii or portions thereof can then be remeasured immediately or later to locate and correct the error.

The program is currently designed to automatically merge the radial growth measurements into an existing stem analysis data file containing heights to each section, and other tree or plot characteristics. The data can be displayed on the screen or printed on a printer by individual sections or for the entire tree. The data can also be plotted in several types of graphs on a dot matrix printer, pen plotter, laser printer, or displayed on the screen if a color/graphics adapter is installed in the microcomputer. Plots of ring widths all formed in the same year versus height (a Duff and Nolan [1953] Type 1 sequence) (Fig. 2) or ring widths at a given height versus age (a Duff and Nolan [1953] Type 2 sequence) (Fig. 3) can be generated, as well as a cumulative height-age curve (Fig. 4), stem taper at various ages (Fig. 5), and a three-dimensional representation of diameter increment, age, and height (Fig. 6).

Plotting the data provides a way of detecting measurement errors, and can aid interpretation. Although at first glance the plot of diameter increment, height, and age (Fig. 6) appears to be quite complicated, it does provide some interesting insights into the growth and development of a tree. By taking "slices" from the surface parallel to the height axis, holding

age constant, one can obtain a Duff and Nolan (1953) Type 1 sequence (Fig. 2). By slicing the surface parallel to the age axis, one obtains a Duff and Nolan (1953) Type 2 sequence (Fig. 3). One can also see that during certain years conditions were not as favorable for diameter growth causing "troughs" running parallel to the height axis. Likewise, one can also see "ridges" which formed when conditions were better. Another interesting aspect is that the maximum diameter increment at each height steadily declines with age. The age at which the maximum diameter at each height occurs tends to parallel that of the cumulative height-age curve.

DISCUSSION

The Tree Ring Measurement System is a self-contained, automated system for measuring radial growth increments. One of the main advantages of the system is its cost; excluding the microcomputer and microscope, the measuring device can be put together for under $2,000 U.S., a fraction of the cost of other systems, while maintaining accuracy. The Digi-Mic includes a cassette recorder and RS-232 interface for data transfer and is available for $11,950 Cdn., without a microcomputer or microscope.

Another advantage of the system is its flexibility. Data are available in a usable form on the microcomputer for additional analyses and can be stored in any format, unlike the pre-specified format of the Addo-X or Digi-Mic. Data are

recorded on paper tape for the Addo-X, and onto cassette for the Digi-Mic, although the Digi-Mic has been connected to Apple and Radio Shack microcomputers (Fayle et al. 1983; Jordan and Ballance 1983). The program includes plotting facilities for graphs comparable to those produced with a program developed by Trimmer and Verch (1983) for mainframe computers using data generated by the Digi-Mic.

Although the movement of the sample is not automatic (the operator must turn the thumb-wheel as opposed to a remote control switch in the Digi-Mic), measurement speed is comparable (Trimmer and Verch 1983). About 12 radii (90 years old, 18 cm long) can be measured in approximately 1 hour. In general, measurement time depends on the average ring width, sample preparation, and microscope quality.

The Tree Ring Measurement System offers significant advantages over other automated systems in terms of cost and flexibility. The software can be configured exactly to the user's requirements, from a simple program to control ring width measurement to a more complex program which can include plotting, editing, and error detecting features. Because of difficulty in bringing stem analysis disks back from the field, the system could be modified to measure growth rings from photographs of the sections (Biging and Wensel 1984) and scale the distances accordingly. However, this method would not be appropriate in cases where the radial increment is quite small, since the photograph would not show the necessary detail. Additional information on hardware and software for the system

may be obtained by writing to the authors. Copies of the software are available for a small handling charge.

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Figure A.1. Tree Ring Measurement System.

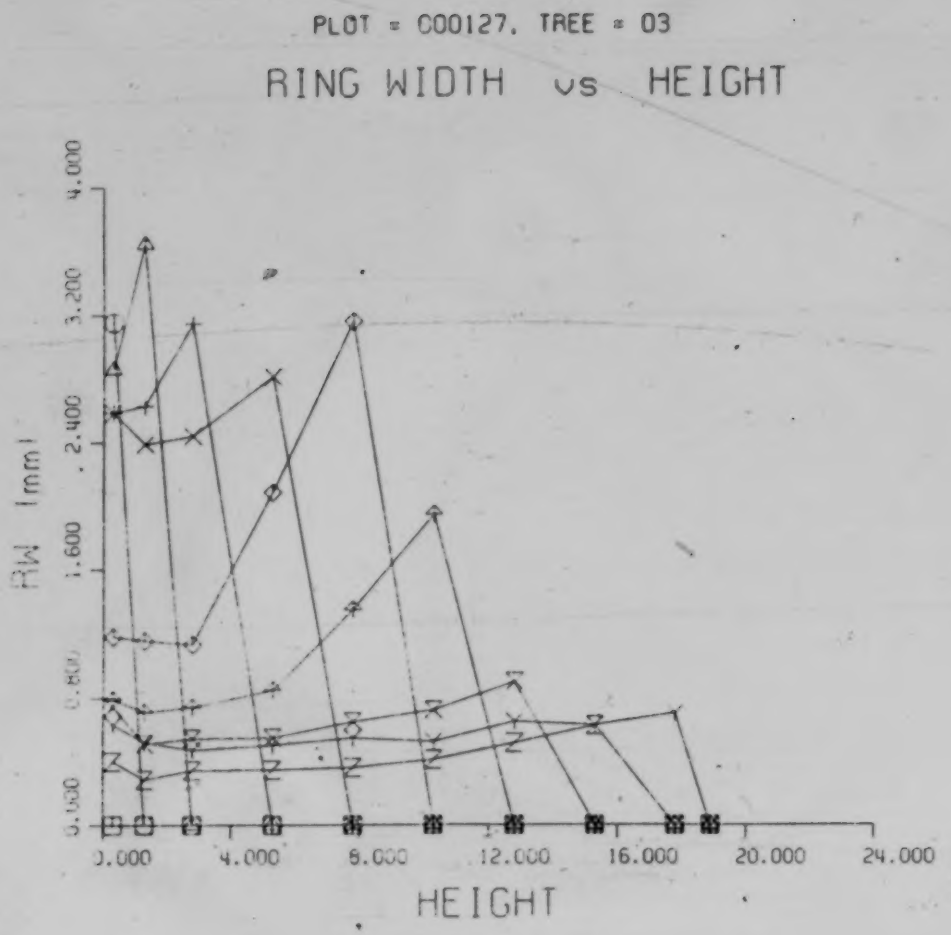

Figure A.2. A Duff and Nolan (1953) Type 1 sequence of the longitudinal distribution of annual radial increment. Plot of ring widths all formed during the same year versus height.

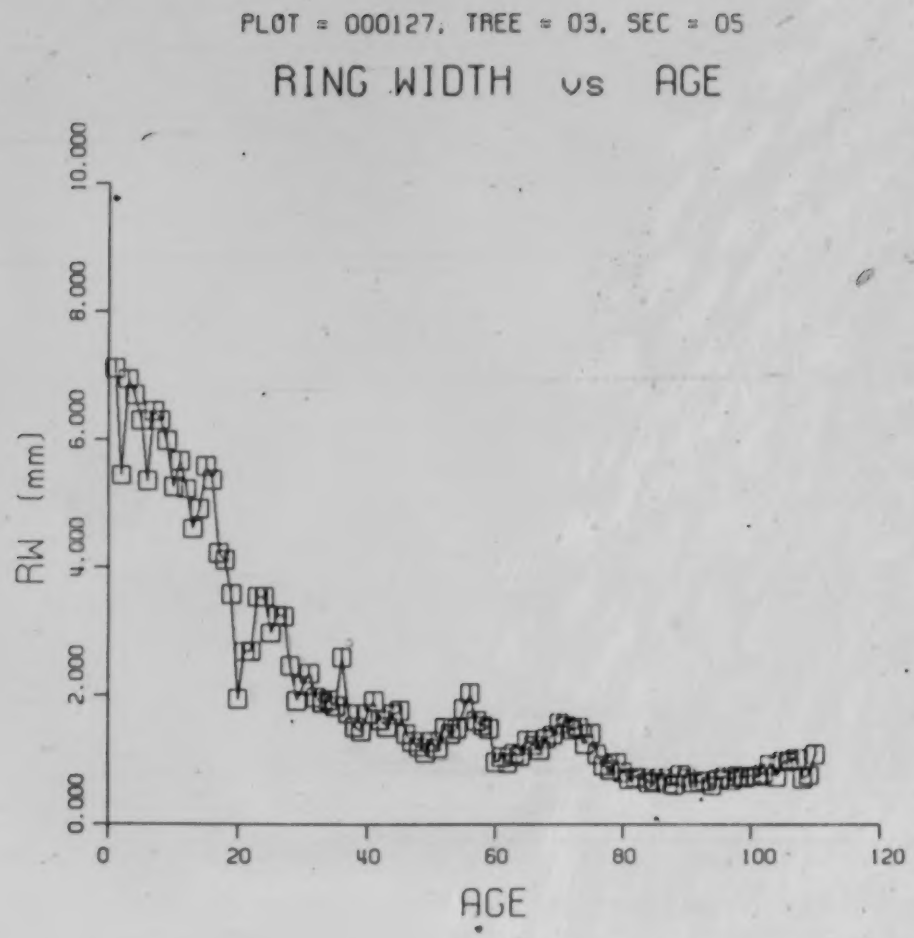

Figure A.3. A Duff and Nolan (1953) Type 2 sequence. Plot of ring widths all formed at the same height versus the number of years from formation.

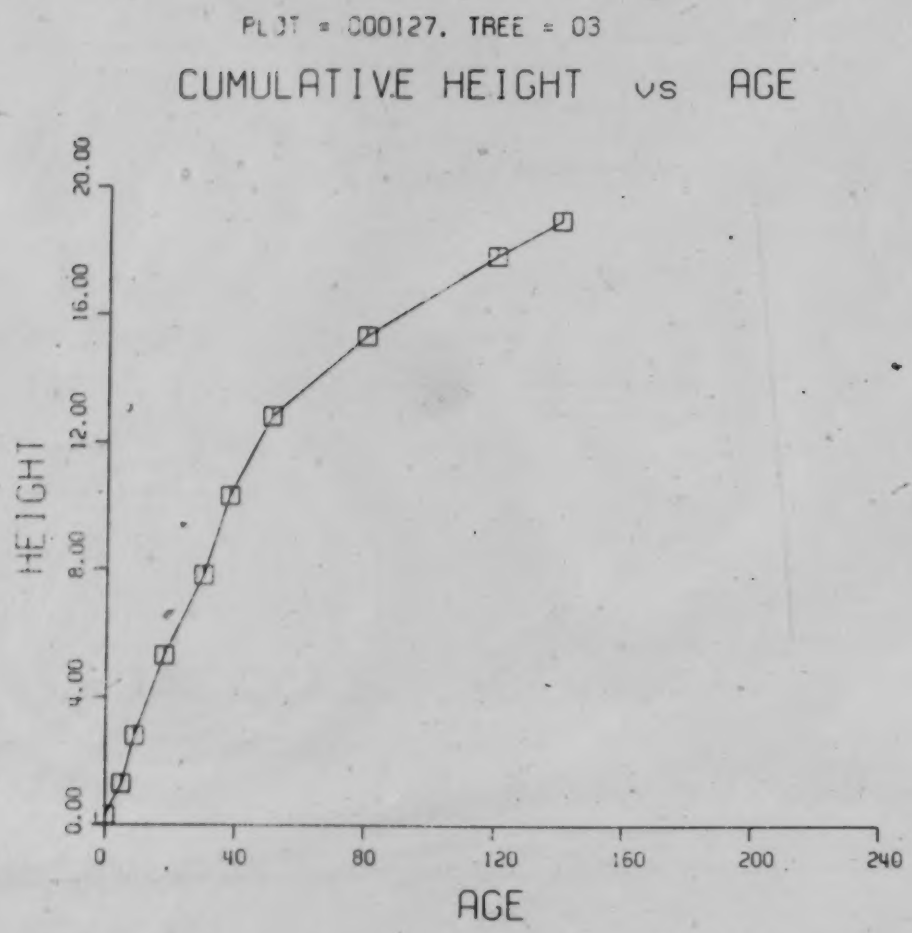

Figure A.4. Cumulative height-age curve.

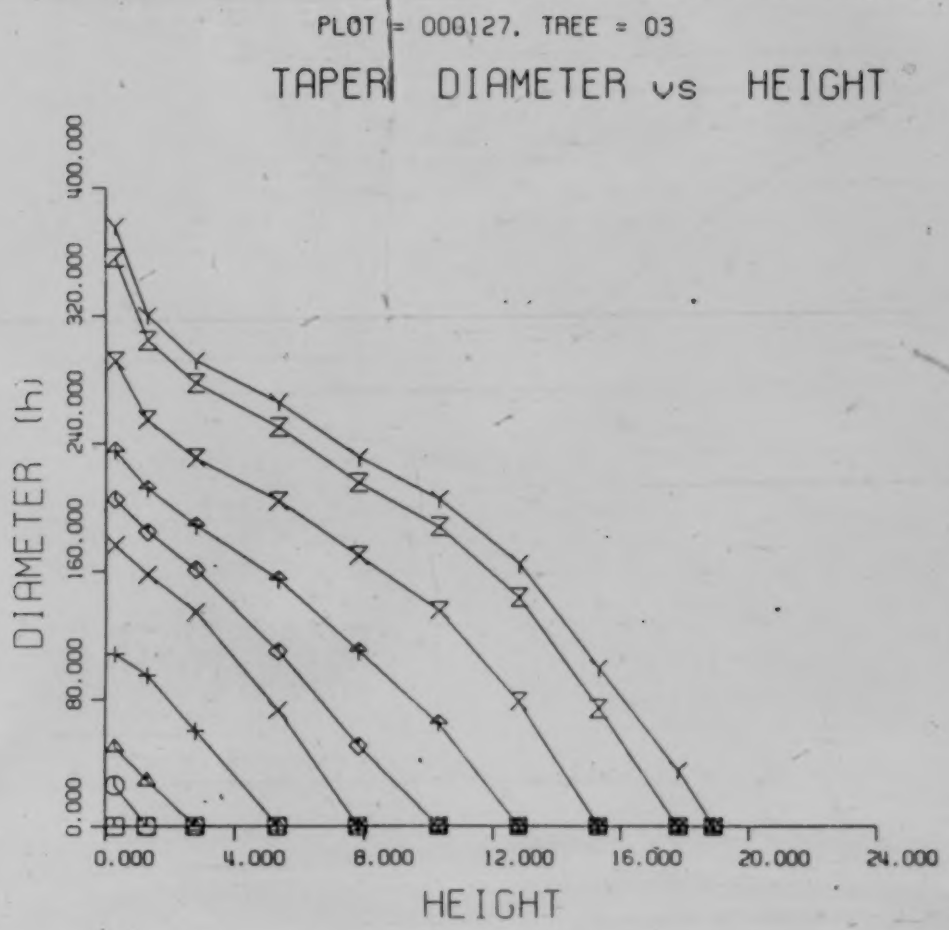

Figure A.5. Plot of stem taper for various ages of the tree.

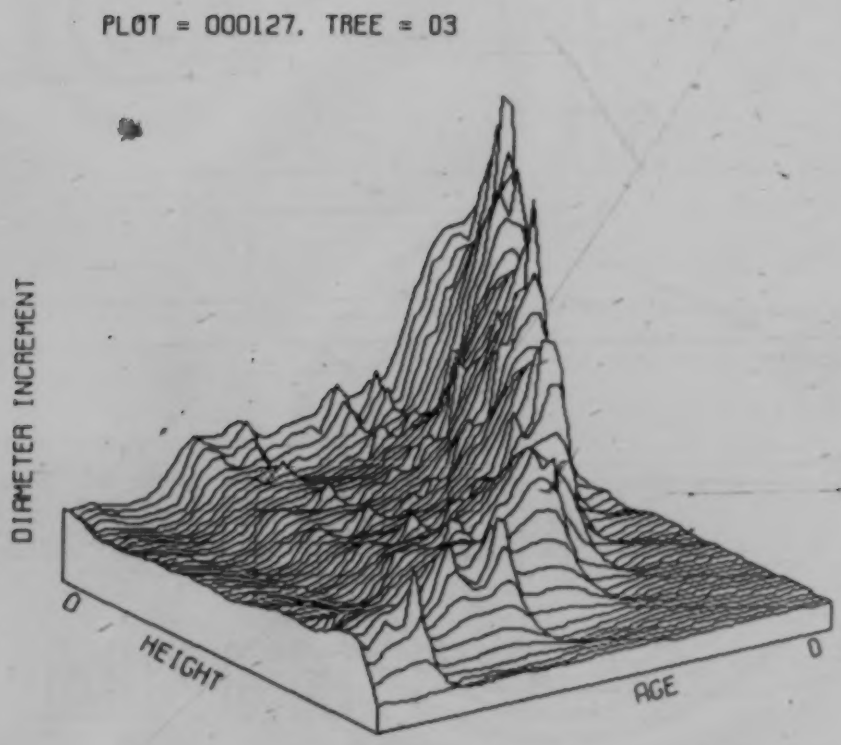

Figure A.6. Three-dimensional representation of diameter increment, height, and age for one tree.

APPENDIX B

DERIVATION OF AN ASYMPTOTIC TAPER MODEL FROM THE CHAPMAN-RICHARDS FUNCTION

Height (h) above the stump relative to the asymptotic height (H_∞) above the stump,

[1] $y = [(h-.3)/(H_\infty-.3)]$,

can be predicted as a function of asymptotic diameter (D_∞) relative to the asymptotic diameter at the stump ($D_\infty(.3)$),

[2] $x = 1 - D_\infty/D_\infty(.3)$,

using the Chapman-Richards growth curve,

[3] $y = A[1- \exp(-cx)]^b$,

with parameters A (the upper asymptote), b, and c. Equation [3] can be rearranged so that D_∞ is the dependent variable. Solving for D_∞, results in the model,

[4] $D_\infty = D_\infty(.3)\{ 1 + (1/c)\ln[1 - (y/A)^{1/b}]\}$.

When h = .3, y = 0, so that $D_\infty = D_\infty(.3)$. By constraining the model to equal zero at the top of the tree, the parameter A can be eliminated. Solving [4] for A when $D_\infty = 0$ and y = 1 yields

[5] $A = [1 - \exp(-c)]^{-b}$.

Substituting for A and y and replacing (1/c) with a gives the final model for the asymptotic taper,

[6] $D_\infty = D_\infty(.3)\{1 + a \ln[1-(1-\exp(-1/a))((h-.3)/(H_\infty-.3))^{1/b}]\}$,

with two parameters a and b.